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Development of Hexagrammids (Pisces: Scorpaeniformes) in the Northeastern Pacific Ocean

Arthur W. Kendall, Jr. and Beverly Vinter

March 1984

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Development of Hexagrammids (Pisces: Scorpaeniformes) in the Northeastern Pacific Ocean

ARTHUR W. KENDALL, Jr. and BEVERLY VINTER[1]

ABSTRACT

Larvae of *Oxylebius pictus*, *Zaniolepis* sp., *Ophiodon elongatus*, *Hexagrammos stelleri*, *H. decagrammus*, *H. lagocephalus*, *H. octogrammus*, and *Pleurogrammus monopterygius* are described and illustrated from field collections which were supplemented by laboratory reared specimens of some species. Larvae hatch at a rather large size (3-9 mm), are heavily pigmented, and undergo direct development to an epipelagic prejuvenile stage. Larvae of the five genera are separable on the basis of body shape, pigmentation, and meristic characters. Larvae of the four species of *Hexagrammos*, which are quite similar in appearance, are separable on the basis of a combination of several pigmentation characters. Developmental evidence indicates that *Oxylebius* and *Zaniolepis* are similar to each other and are more similar to presumed primitive cottids than the other included genera. *Ophiodon* is dissimilar to the other four genera. *Pleurogrammus* and *Hexagrammos* have similar appearing larvae. Among the species of *Hexagrammos* a progression of increasing larval pigmentation can be seen from *H. stelleri* to *H. decagrammus*, *H. lagocephalus*, and *H. octogrammus*.

INTRODUCTION

The scorpaeniform family Hexagrammidae, the greenlings, (sensu Rutenberg 1962) is an exclusively North Pacific group of fairly common generally demersal fishes of the continental shelf that range in maximum size from *Oxylebius pictus* (25 cm) to *Ophiodon elongatus* (150 cm) (Hart 1973). The life history pattern observed in species (*Oxylebius pictus* [DeMartini 1976]; *Ophiodon elongatus* [Giorgi 1981]; *Pleurogrammus monopterygius*, *Hexagrammos* spp. [Gorbunova 1962]) studied so far, is to lay demersal eggs in nests, which are guarded by the male. An epipelagic prejuvenile stage (Hubbs 1943) occurs during development of most hexagrammids (Gorbunova 1962). Substantial fisheries exist for lingcod, *O. elongatus*, and Atka mackerel, *Pleurogrammus monopterygius* (U.S. Department of Commerce 1981).

Two major systematic revisions of the group (Quast 1960; Rutenberg 1962) resulted in several disagreements regarding the status of certain species and genera and the limits of the family. Evidence presented herein indicates that larval morphology may assist in resolving these disagreements.

The only major previous work on larval descriptions of hexagrammids was by Gorbunova (1962) who illustrated larvae of 10 species and described in detail 8 of them (Table 1). Material dealt with here amplifies two descriptions presented by Gorbunova (1962), corrects two of her identifications, and provides descriptions of two species not detailed in her work. Other descriptive work on larval hexagrammids has dealt with single species and will be discussed with the species in question or in the discussion.

MATERIALS AND METHODS

Most specimens used as the basis of this paper were collected in plankton tows made during cruises off the Pacific coast of the United States by personnel of the Northwest and Alaska Fisheries Center (NWAFC) and the Southwest Fisheries Center. Larvae of *Hexagrammos stelleri* and *H. decagrammus* were reared from eggs collected in nests in Puget Sound. A few larval specimens from a variety of rearing and sampling programs along the U.S. Pacific coast were used as auxiliary material. Larval specimens were fixed and stored in 3-5% formaldehyde solutions buffered with sodium borate. Adult material from the U.S. National Museum, University of Washington School of Fisheries, and NWAFC ongoing groundfish surveys was examined for meristic and osteological information.

We attempted to establish two series of five larvae in each millimeter size interval from hatching to the definitive complement of dorsal and anal fin rays. One series was cleared and stained following Dingerkus and Uhler (1977) to trace cartilage and bone formation. The other series was used for morphometric measurements. Limited material was available, so less than complete series were used in some cases. Some specimens were used first in the morphometric series and then cleared and stained. With the cleared and stained series, notes were made on the presence and shape of various skeletal elements and which meristic features were stained either blue (cartilage) or red (bone). Bones were said to have attained their adult shape when they were entirely red and showed sharp definitive edges.

The vertebral centrum immediately anterior to the urostyle is called preural centrum 2 in keeping with common practice (Potthoff 1980), although no fusions of separate elements were seen in the development of the urostyle. The following measurements were made in millimeters using an ocular micrometer in a dissecting microscope once the feature was formed on the left side of larvae in the morphometric series:

Standard length (SL): Tip of snout to tip of notochord in larvae before flexion is complete (some consider this notochord length [Potthoff 1980]), to posterior margin of hypural elements in postflexion larvae.

Preanal length: Tip of snout to middle of anus.

Head length: Tip of snout to posterior margin of opercle.

Snout length: Tip of snout to anterior margin of eye.

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Table 1.—Summary of previous descriptions of young stages of hexagrammids and material examined in this study.

Taxon	Previous descriptions		Material used in this study							
			Pigment		Morphometrics		Meristics		Detailed osteology	
	References	Comments	No.	Length range (mm)	No.	Length range (mm)	No.	Length range (mm)	No.	Length range (mm)
Oxylebius pictus	Gorbunova 1962	Discussed 6.3-7.3 mm larvae; illustrated a 7.6 mm specimen, probably actually *Hemilepidotus* sp.	[1]50	4.5-20.8	10	7.9-20.8			4	9.3-15.0
Zaniolepis sp.	Gorbunova 1962	Discussed 5.2-6.5 mm larvae; illustrated a 6.7 mm specimen as *Zaniolepis latipinnis*; probably actually *Hemilepidotus* sp.	30	2.5-44.4					1	13.3
Ophiodon elongatus	Blackburn 1973	Discussed pigment on a 10.3 mm larva, illustrated 8.9, 12.5, and 17 mm larvae.	[1]>100	9.0-52.0	83	9.0-52.0	30	9.5-28.9, 40.0	8	9.5-28.9
	Marliave 1975	Illustrated and briefly described 9.0-55 mm (TL) specimens.								
	Phillips and Barraclough 1977	Discussed larval pigment and metamorphosis briefly; illustrated 7 specimens 7-80 mm.								
Hexagrammos stelleri	Gorbunova 1962	Illustrated and described 10.1-61.5 mm specimens.	[2]>100	7.8-61.0	104	7.8-61.0	35	8.3-49.5	7	8.3-29.0
Hexagrammos decagrammus	Gorbunova 1962	Illustrated and described 8.7-16.7 mm larvae as *H. superciliosus.*	[2]>100	7.4-55.5	100	7.4-55.5	29	12.0-25.6	7	8.6-30.1
	Marliave 1975	Illustrated and briefly described reared 7-13 mm (TL) larvae.								
Hexagrammos lagocephalus (lagocephalus)	Gorbunova 1962	Illustrated (eggs and 12.6-23.0 mm larvae) and described from material west of long. 170°W. Distinct from larvae here described as *H. lagocephalus.*								
Hexagrammos lagocephalus (superciliosus)	Gorbunova 1962	Illustrated and described 12.0-65.0 mm specimens as *H. decagrammus.*	>100	8.5-34.3	55	8.5-34.3	18	9.9-28.0	6	9.1-28.0
Hexagrammos octogrammus	Gorbunova 1962	Illustrated and described eggs and 7.1-46.0 mm specimens.	>100	7.5-47.0	91	7.5-47.0	36	8.0-45.0	7	8.0-29.5
Hexagrammos otakii	Gorbunova 1962	Illustrated and described eggs and 6.7-17.8 mm larvae.								
Hexagrammos agrammus	Fukuhara 1971	Illustrated and described reared eggs and 8.6-10.2 mm larvae. [In Jpn.]								
Pleurogrammus monopterygius (azonus)	Gorbunova 1962	Illustrated and described eggs and specimens (8.0-88.0 mm).								
	Hattori 1964	Illustrated and described 10.0-32.0 mm specimens. [In Jpn.]								
	Yusa 1967	Illustrated and described reared eggs and early larvae (8.5-10.6 mm).								
Pleurogrammus monopterygius (monopterygius)	Kobayashi 1958	Illustrated and described 25.7-44.4 mm specimens. [In Jpn.]	>100	9.7-76.0	84	9.7-76.0	43	9.7-28.1	8	9.8-28.1
	Gorbunova 1962	Illustrated and described eggs and specimens (10.5-30.0 mm).								

[1]Includes reared yolk-sac larvae.
[2]Includes complete reared larval series.

Eye width: Maximum horizontal distance through eye.

Body depth at pectoral base: Depth of body (exclusive of dorsal fin structures) at insertion of pectoral fin.

Body depth at caudal peduncle: Minimum body depth between insertion of dorsal and anal fins and origin of caudal fin.

Snout to dorsal fin length: Tip of snout to origin of dorsal fin.

Snout to anal fin length: Tip of snout to origin of anal fin.

Snout to pelvic fin: Tip of snout to origin of pelvic fin.

Measurements were grouped by 1 mm SL intervals and the means of the measurements within each interval were plotted as percentage of the mean of SL or head lengths within the interval. A computer generated best nonparametric fit curve based on all the data points was drawn (see Appendix Figures 1-10). Using percentages rather than actual measurements emphasizes changes in relative size of features during ontogeny and allows easy visual comparison of plots among species. Limited material of *Oxylebius pictus* and *Zaniolepis* sp. prevented such treatment of their morphology.

Terminology for subdivisions of the larval stage follows Sumida et al. (1979). In development of hexagrammids, there is no abrupt metamorphosis at the end of the larval period. Rather the fish remain epipelagic and continue to grow after fin formation is complete. During this stage the fish generally have a pigment pattern in life of a dark green/blue dorsum and a silvery ventrum. These fish thus match the definition of prejuvenile given by Hubbs (1941, 1943) as do young of several other families (e.g., Mullidae [Caldwell 1962], Pomatomidae [Kendall and Walford 1979], and Mugilidae [Anderson 1958]). These prejuvenile hexagrammids are frequently caught in neuston nets in the North Pacific, and therefore we will describe them along with the larvae. There is no definite point of transition from larva to prejuvenile. Associated with assuming the demersal habits of the adults, the prejuveniles presumably undergo rapid changes in morphology and pigment to become miniature adults (juveniles), as happens in young mullids (Hunter 1967).

Specific larvae representing the developmental series of each species were drawn with the aid of a camera lucida attached to a dissecting microscope. The least damaged and distorted larvae were selected for illustration; however, the posture of some was not ideal. Limited changes in posture were drawn in, to avoid further distortion. The drawings were modified if examination of comparable larvae showed that any substantive features of the illustrated larva were not representative of the rest of the material on hand.

Specific identifications of the series were made by comparison with reared material of known parentage when possible. Pigment patterns and rates of development proved to be the most useful characters in establishing series. Counts of meristic features on larger larvae in the series linked them to the appropriate adults (Table 2). The most useful meristic features were the number of dorsal and anal fin rays, principal caudal fin rays, and myomeres (vertebrae). Geographic occurrence provided substantiating evidence for identification in some cases.

RESULTS

Hexagrammid larvae range from about 3 to 9 mm at hatching. They are heavily pigmented with scattered melanophores over most of the body, particularly dorsally. More, similar pigment is added during larval development. The larvae are rather elongate but plump in cross section, with large round eyes. *Ophiodon elongatus* has a pointed snout and large terminal mouth. In the other hexagrammid larvae the head is blunt and the mouth is terminal to subterminal and is upturned when closed. It appears small in side view, not extending beyond the middle of the eye, but the size of the gape is substantial because the head is so broad. Development from hatching to juvenile is direct without remarkable changes in body form or unusual fin development. In most species the sequence of formation of definitive counts of meristic elements is as follows: Branchiostegal rays, lower-limb gill rakers, caudal fin rays, pectoral fin rays, vertebrae, second dorsal and anal fin rays, and first dorsal and pelvic fin rays. The neural and hemal arches form before their associated vertebral centra and ossification of the individual centrum begins dorsally and ventrally as saddle-shaped pieces of bone at the bases of the neural and haemal elements. Ossification proceeds laterally as the pieces join each other to form rings which make up the centrum. Several partially ossified vertebrae could be present at once. Vertebrae ossify from anterior to posterior, except the urostyle ossifies before most other vertebrae.

Oxylebius pictus (Painted Greenling) Figures 1 and 2, Table 3

DeMartini (1976) and DeMartini and Anderson (1980) described the reproductive biology of this colorful, small, demersal fish of nearshore rocky habitats that ranges from Baja California to Alaska. Males establish spawning sites during warmer months where they guard egg masses deposited by one or more females. The planktonic larval period may last 1-3 mo after which the juveniles are recruited to rocky substrates. Gorbunova (1962) discussed larvae 6.3-7.3 mm long and illustrated a 7.6 mm specimen that appears more similar to larvae of *Hemilepidotus* sp. (see Richardson 1981) than to those to be described here as *O. pictus.*

Larvae hatched and were maintained in the laboratory for several days from an egg mass of *O. pictus* that was collected by diving in Puget Sound, Wash. Similar distinctive larvae (with highly pigmented pectoral fin buds) occurred in plankton

Table 2.—Adult meristic characters of northeast Pacific hexagrammids. For all species the normal count for branchiostegal rays is 6 and for pelvic fin rays is I,5. Caudal fin ray data from the present study; other data from Quast (1960) except as noted.

	Vertebrae		Fin rays								
			Dorsal				Caudal[1]				
							Dorsal		Ventral		
Species	Precaudal	Caudal	First (spines)	Second (softrays)	Anal	Pectoral	Secondary	Principal	Principal	Secondary	First arch gill rakers
Oxylebius pictus	13-15	23-25	15-17	13-16	14-17	14-17	9	7	6	9	11-14
Zaniolepis frenata[2]	14-15	26-28	21	12	18-19						
Zaniolepis latipinnis[3]	14	28	21-22	11-12	18-20	14	6- 8	7	6	7- 9	11-12
Ophiodon elongatus	23-24	33-35	25-28	19-21	21-25	16-18	13-15	7	7	12-14	19-28
Hexagrammos stelleri	20-22	31-34	22-25	18-22	22-25	18-20	16-17	7	8	14-15	16-20
Hexagrammos decagrammus	20-22	33-35	21-23	22-26	23-26	18-20	12-16	7	9	12-14	15-20
Hexagrammos lagocephalus	20-23	32-34	20-23	20-25	21-24	18-21	17-22	7	10	15-19	14-18
Hexagrammos octogrammus	18-19	32-35	18-20	22-25	23-26	18-19	15-17	7	8	14-15	14-17
Pleurogrammus monopterygius	26-28	32-35	21-24	24-30	23-28	23-28	16-19	8	11	16-20	22-27

[1]Principal caudal fin rays are supported by the hypurals and parhypurals.
[2]Miller and Lea (1972); vertebrae: Clothier (1950).
[3]Miller and Lea (1972); vertebrae: Rutenberg (1962).

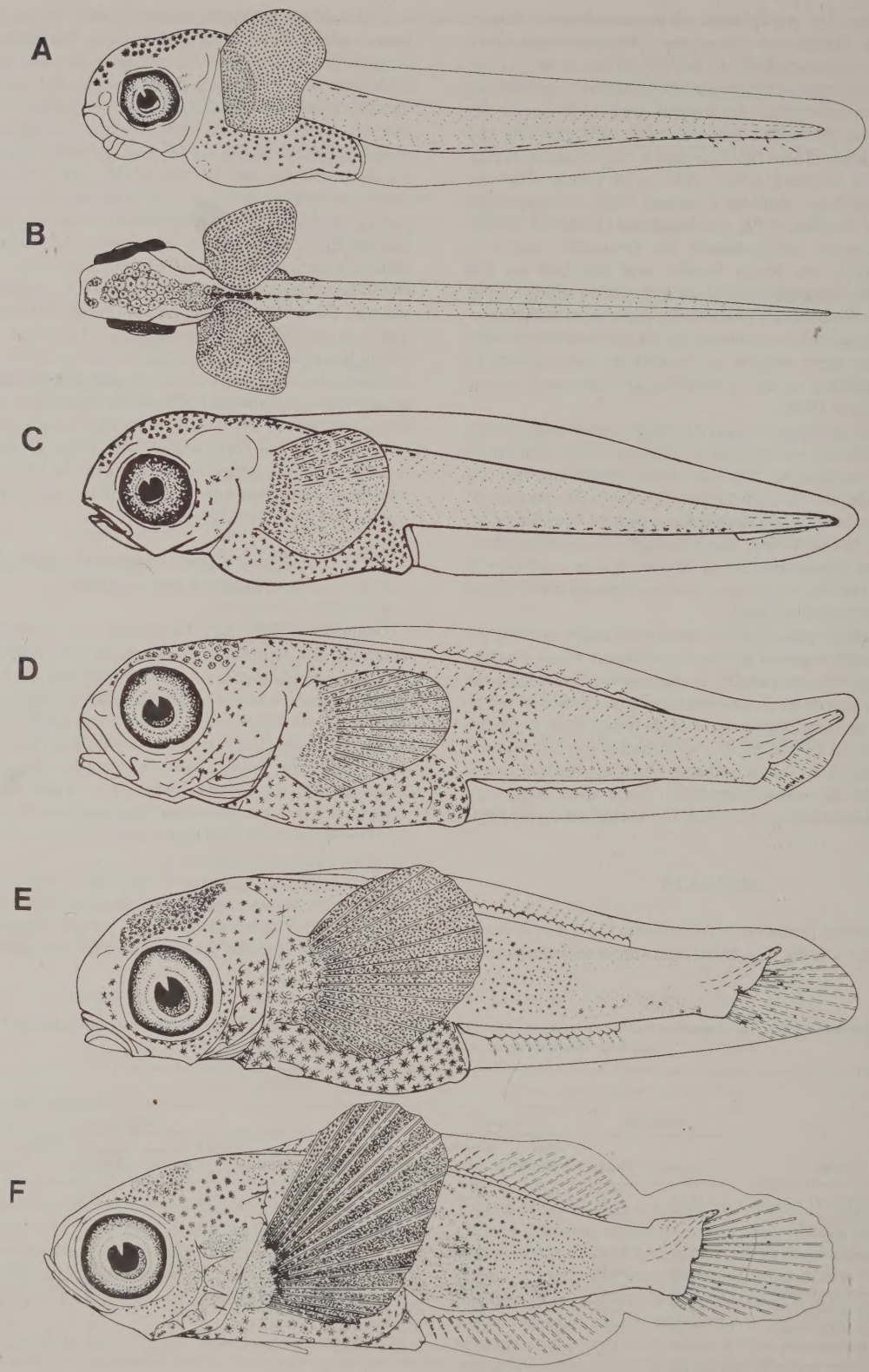

Figure 1.—Larvae of *Oxylebius pictus*: A. 4.5 mm, B. 4.5 mm (dorsal view), C. 6.0 mm, D. 7.4 mm, E. 8.5 mm, F. 10.5 mm.

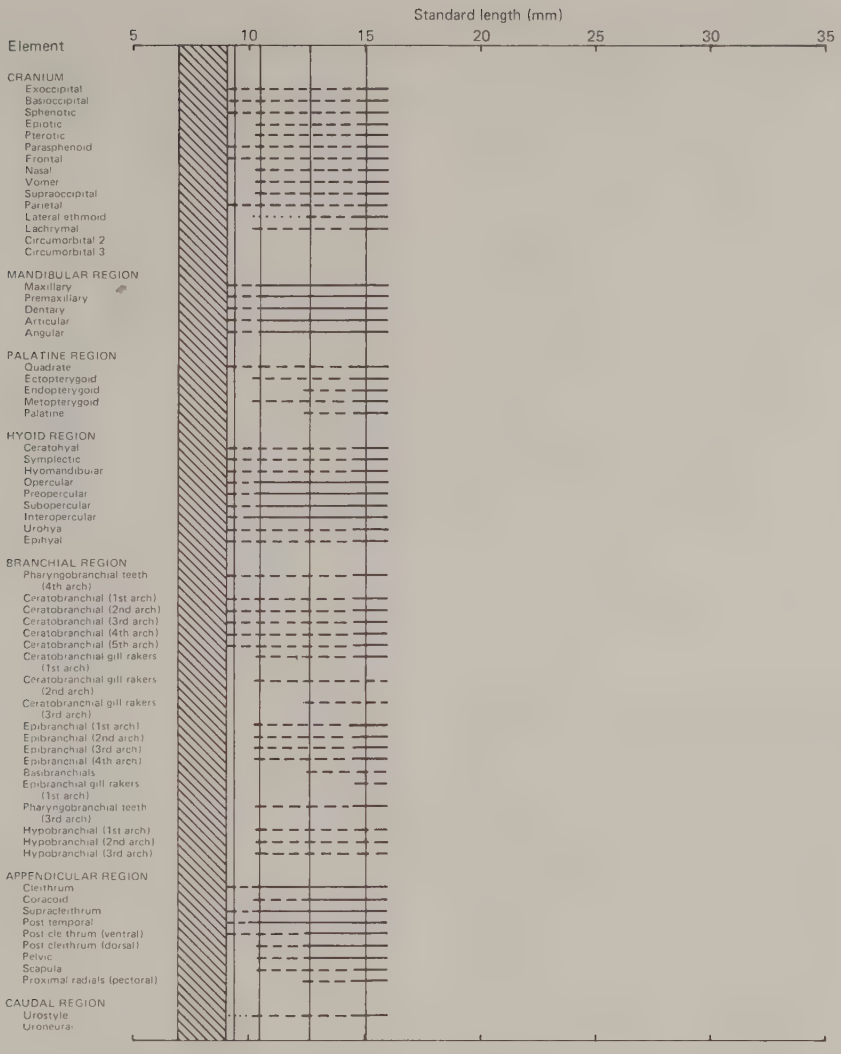

Figure 2.—Ossification of major bones in *Oxylebius pictus*. Vertical lines represent specimens examined. Hatched area represents flexion. Horizontal lines: Dotted section represents element present as cartilage, dashed section represents element partially ossified, solid line represents element with definitive ossified shape.

samples from California, that included larger specimens that had developed the meristic characteristics of *O. pictus*.

Pigmentation—On hatching at 4-5 mm the larvae have large pectoral fin buds heavily pigmented with small melanophores (Fig. 1). The melanophores cover the internal base and membrane of the fin only but show through this thin tissue to the external side of the fin. The dorsal surface of the brain is covered with stellate melanophores whose extended edges touch each other and which are concentrated over the olfactory and optic lobes and the hindbrain. The pigment over the hindbrain narrows posteriorly to a line of melanophores in the middorsal septum which ends over the gut. A ledge of pigment visible through the otic capsule appears to line its floor. The gut cavity is densely covered with evenly spaced melanophores except along the ventral midline, which is unpigmented. Trunk pigment is limited to a continuous line of melanophores along the ventral midline; the line originates about five myomeres posterior to the anus and terminates at the tip of the notochord where it spreads into the finfold. By 7 mm pigment has been added to the opercular region and to the external surface of the pectoral fin bud, and the ventral part of the gut is pigmented across the midline. Pigment has also been added to the trunk as a diffuse patch of melanophores over the side of the body between the bases of the just-forming second dorsal and anal fins. This patch becomes larger during development and joins the pigment at the back of the head so that by 10 mm the anterior part of the body posterior to the dorsal and anal fin insertions is uniformly and densely pigmented. A few melanophores are scattered on the developing caudal fin rays, but the dorsal and anal fin rays and fin membranes are unpigmented. By about 16 mm the beginning of the banded pigment pattern on the trunk, characteristic of the adult, is seen and this pig-

Table 3.—Larval characters that allow distinction between *Oxylebius pictus* and *Zaniolepis* sp. Too few specimens were available to quantify some character states to the degree desirable, so relative statements must suffice.

Character	Character state	
	Oxylebius pictus	*Zaniolepis* sp.
3-7 mm SL		
Presence of pigment		
On isthmus	no	yes
Laterally above gut	less	more
On ventral midline of trunk	more	less
On tip of snout and onto tip of palate	no	yes
On internal surface of pectoral fin base	yes	no
On lower lip	no	sometimes
Morphology		
Eye size	smaller (<20% head length)	larger (>30% head length)
Preanal finfold	no (>5 mm)	yes (<8 mm)
Pectoral fin length	reaches anus by 8.0 mm	reaches anus by 5.5 mm
Notochord flexion	7-9 mm	5-7 mm
Dorsal indentation on eye	no	yes
>7 mm SL		
Spiny scales cover body	no	yes
Body shape	stout (<30% SL)	slender (<25% SL)

ment extends onto the base of the dorsal fin. Through the largest pelagic sizes on hand (20 mm) the pectoral fins are densely pigmented and the caudal peduncle and caudal fin are practically unpigmented. The tip of the snout and the lips remain unpigmented throughout the pelagic stage.

Morphology—The most outstanding feature of *O. pictus* larvae is the large, pigmented pectoral fins. These increase in size relative to the body as the larvae grow. By about 8 mm they extend to the level of the anus, and they continue to grow, reaching the middle of the anal fin by 11 mm. The notochord flexes at 7-9 mm. Pelvic fin buds are already present in flexion larvae. Body parts of a series of 10 specimens from 7.9 to 20.8 mm were measured. As percentages of SL the proportions of various parts changed during this length interval as follows: Total length increased from 106 to 125; preanal length fluctuated from 54 to 64; head length fluctuated from 31 to 42; body depth at the pectoral base increased from 29 to 34; depth at the caudal peduncle increased from 7.8 to 13; snout to anal fin origin fluctuated from 55 to 64 (larvae > 8.6 mm); snout to dorsal fin origin remained at 31-35 (larvae > 8.6 mm); and the snout to pelvic fin increased from 29 to 37. As a percentage of head length the proportion of other body parts changed during this length interval (7.9-20.8 mm) as follows: Snout length increased from 20 to 23; and eye diameter decreased from 41 to 32. Thus *O. pictus* larvae, relative to the other larvae discussed in this paper except *Zaniolepis* sp., have larger heads, develop larger caudal fins, are deeper bodied, and have longer preanal lengths (see Appendix Figures 1-10). Too few specimens of *Zaniolepis* sp. were available for conclusive comparisons, but they appear to have similar proportions to *O. pictus*, except the latter have deeper bodies and smaller eyes.

Developmental Osteology—Only four of our limited supply of *O. pictus* larvae were cleared and stained. In a flexion larva (9.3 mm SL), all principal caudal rays are ossified, but the rest of the fins have only partial complements of developing unossified fin rays. The vertebrae are forming from anterior to posterior with the first 10 as complete rings, succeeded by 9 partial rings. The anterior 29 neural spines have ossified, as well as appropriate coordinate hemal spines. In the head region, the six branchiostegal rays are formed; there are three preopercular spines and a spine on the posttemporal. By 10.4 mm the notochord has completed flexion and fin rays are approaching their adult complements. The anterior 32 vertebrae are ossified as well as their associated neural and hemal spines. By 12.7 mm there are five preopercular spines and an interopercular spine as well as a posttemporal and supracleithral spine. In the hypural region two plates are ossified each with a foramen, indicating fusion of hypural 1 with hypural 2 and hypural 3 with hypural 4. Complete rings are present for the anterior 38 vertebrae followed by 3 with incomplete rings. Lower limb gill rakers have increased to five.

Ossification appears to be nearly complete in a 15.0 mm specimen. All meristic features, except gill rakers, possess their adult complements of elements. The head spines seen on the 12.7 mm specimen are well developed and a second supracleithral spine is present. The hypurals are ossified. Hypural 5 is present, there is a small slit in the dorsal hypural plate (left from the fusion of hypurals 3 and 4), and there is a pronounced foramen in the ventral hypural plate. Three epurals can be seen, but only the posterior one is stained and that with Alcian Blue. There is no neural spine on the urostyle, but preural centrum 2 has two shortened neural spines (specialized neural arches). One pair of uroneurals is present. There are 7 + 6 principal caudal fin rays and 7 dorsal and 6 ventral secondary caudal fin rays.

Ossification of most skeletal elements occurs in a similar sequence to that in other hexagrammids. Development of bones has already started on larvae smaller than the smallest one that was cleared and stained (9.3 mm, undergoing notochord flexion). On the 9.3 mm specimen, the major bones of the cranium, jaws, hyoid arch, and pectoral girdle have begun ossification. The pharyngobranchial teeth and the ceratobranchials are formed. By the end of flexion (10.5 mm), as in *Hexagrammos* larvae, the bones of the jaws and in the opercular series have assumed their adult shapes. Nearly all of the skeletal elements have begun ossification by this stage. Late forming bones, which begin ossification well after notochord flexion and do not assume adult shape until near the end of the larval period (15.0 mm), include the prefrontal, the palatine and bones of the pterygoid series, several bones of the branchial arches, the scapula, and proximal pectoral radials.

Zaniolepis (Combfish)
Figure 3, Table 3

This genus contains two species of rather small (maximum 30 cm), uncommon demersal fishes occurring from Baja California to southern Oregon (*Z. frenata*) and from Baja California to British Columbia (*Z. latipinnis*) in shallow waters to 400 m (Miller and Lea 1972). Little is known of their life history (Johnson and Adams 1970). Alternative classifications have put these fish in separate genera (Rutenberg 1962: *Xantocles frenata* and *Z. latipinnis*) and in their own family (Quast 1960: Zaniolepidae). Although larvae on hand of *Zaniolepis* cannot be correlated with certainty with either species, we suspect we have only one species, since there is little variation among specimens in larval characters. The larvae are quite similar to *O. pictus* in pigment and morphology.

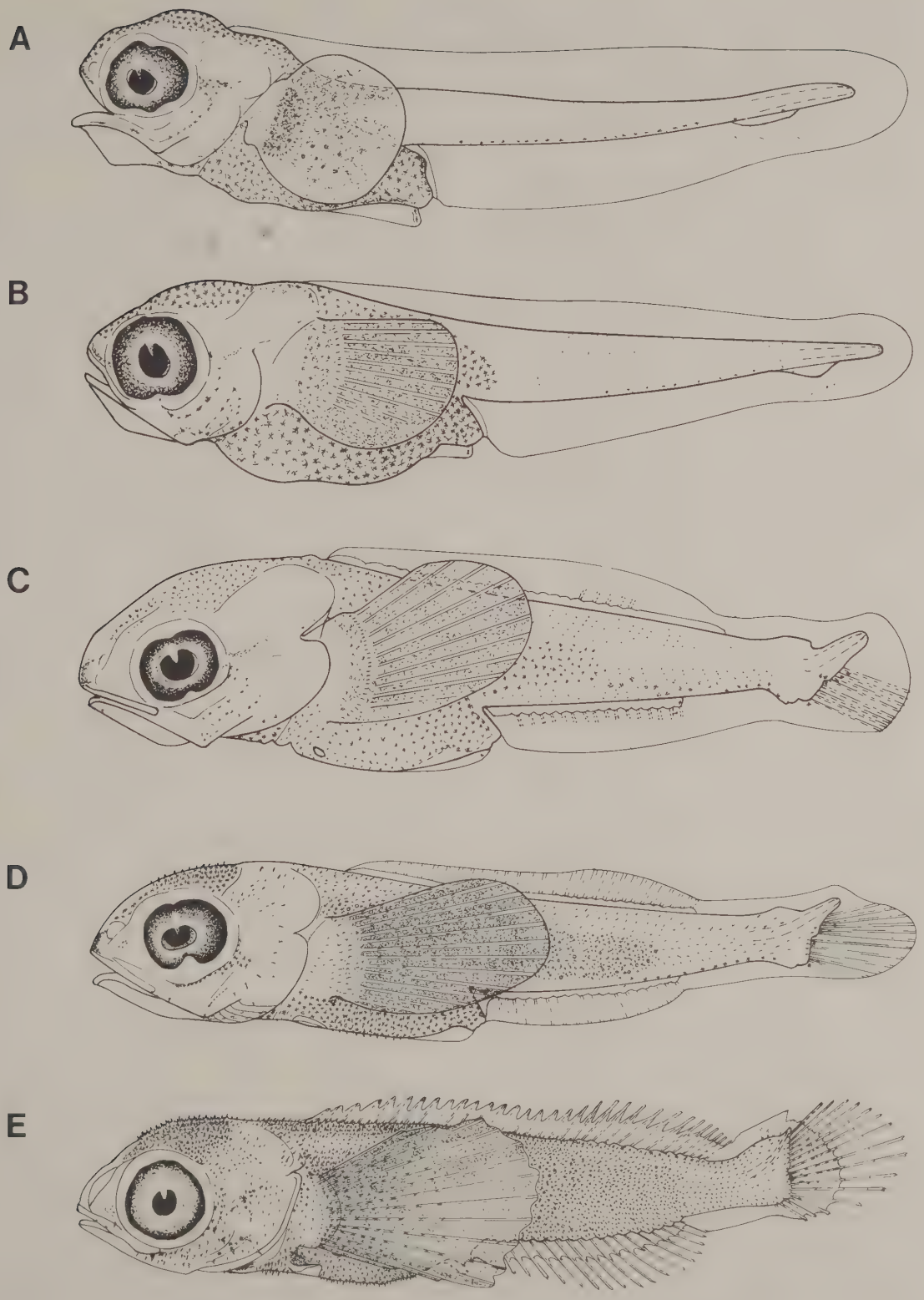

Figure 3.—Larvae of *Zaniolepis* sp.: A. 4.0 mm, B. 5.0 mm, C. 6.2 mm, D. 7.7 mm, E. 9.5 mm.

Gorbunova (1962) illustrated a 6.7 mm larva as *Z. latipinnis* collected off California and described specimens from 5.2 to 6.5 mm long. The illustrated larva appears more like one of *Hemilepidotus* sp. (Richardson 1981) than of the *Zaniolepis* sp. in our collection. The larvae Gorbunova (1962) discussed were too small to have definitive meristic characters to allow unquestioned identification.

The larvae described here were collected in plankton tows off California. Definitive meristic characters of the genus are formed on specimens 10 mm long. Pigment patterns and general morphology of these specimens is seen in smaller specimens in the series which have not yet developed adult meristic complements. The most outstanding feature of these larvae is the presence, in specimens as small as 7 mm, of fine, spiny scales on the body that give the skin of the adult a characteristic texture. These larvae are very similar to those of *O. pictus* in body shape and pigmentation, including the heavily pigmented pectoral fins. Only features brought out by careful examination will distinguish small larvae of *Zaniolepis* sp. from those of *O. pictus* (Table 3). The presence of snout pigment in *Zaniolepis* sp. and its absence in *O. pictus* are readily observable and diagnostic. The external surface of the base of the pectoral fin is pigmented by 7 mm in *O. pictus*, but remains practically unpigmented until at least 13 mm in *Zaniolepis* sp. Inadequate material was available for more than a general description of development.

Pigmentation—On the smallest larvae on hand (2.5 mm) a distinctive pigment pattern is evident that persists throughout the larval period (Fig. 3). Numerous small, closely spaced melanophores give a pigmented appearance to the anterior half of the larvae. Some spots are present in the opercular region and the top of the head is uniformly covered with melanophores, except for a less pigmented patch over the optic lobes of the brain in some. This pigment extends anteriorly to the tip of the snout and continues onto the palate. Posteriorly it covers the nape and spreads onto the flank of the abdominal region and is continuous with pigment covering the lateral surface of the gut. The hindgut is covered with more closely spaced melanophores. Ventrally, pigment crosses the midline in the cleithral and isthmian regions but is absent in the midgut region. A few spots are present in the midventral septum of the trunk. The internal surface of the bases and blades of the pectoral fins are heavily pigmented with fine melanophores. The most noticeable change in larvae up to 7 mm is the extension of the lateral pigment to about 10 myomeres posterior of the anus, mainly on the ventral part of the body. This area of pigment continues to enlarge, and by 10 mm the trunk anterior to the caudal peduncle is covered with melanophores. As this happens the anterior ventral midline melanophores disappear. Median fin pigment is confined to a few melanophores on the principal caudal fin rays and fin membrane. In 14-24 mm specimens the trunk is uniformly densely pigmented to the base of the caudal fin, and the pectoral fins are even more densely pigmented. The external surface of the bases of the pectoral fins is practically free of pigment throughout the series on hand.

Morphology—Larvae of *Zaniolepis* sp. are slender with a moderately short gut. The smallest larvae on hand (2.5 mm) still have yolk and are presumed to have hatched near that size. The pectoral fins are large throughout larval development and develop rays at 5 mm, before notochord flexion, which occurs at about 6 mm. At that time the central principal caudal fin rays are visible and the dorsal and anal fin bases have started to form. Pelvic fin buds are also present. By 8 mm most median fin rays are countable, except for secondary caudal rays. The pelvic fins remain as small buds until rays develop at about 12 mm. The spiny scales characteristic of the adult are first seen on the head and abdominal region of larvae 6.5-7.0 mm. By 9.5 mm they cover the entire body except the snout and extend onto the fin membranes of the pectoral and caudal fins. A small preanal finfold is present in larvae up to about 8 mm, and the hindgut is slightly enlarged and protrudes from the body. The eye is relatively smaller than that of *O. pictus* and tends to have an indentation dorsally in larvae < 9 mm.

Developmental Osteology—From the limited number of specimens available, a 13.3 mm larva that was cleared and stained has adult values of all meristic characters except gill rakers. The first two anal rays appear as weak spines, and the dorsal spines do not appear fully developed, so their relative lengths, which are identifying characters in adults, cannot be determined. Spiny scales cover the entire body, all fins, and most of the head. Several bones of the head are spine bearing. There is one spine each on the nasal, on infraorbital 3, and on the interopercle. Infraorbital 1 (lachrymal) has five spines along its ventral margin and one produced out of the center of the bone. The posttemporal has a bifurcate spine with the anterior point being smaller than the posterior point. There are two small spines on the supracleithrum. The left preopercle has six spines and the right has seven. It is quite possible that more and/or elaborate head spines develop later.

In the caudal region, ossification appears incomplete (e.g., there are no epurals, and no modified neural arch on preural centrum 2); however, it seems that the parhypural and hypurals 1 and 2 are fused, hypurals 3 and 4 are fused, and there is no indication of hypural 5. A pair of small uroneurals is present.

Ophiodon elongatus (Lingcod)
Figures 4 and 5, Table 4, Appendix Figures 1-10

Ranging from Baja California to the northern Gulf of Alaska, this large (maximum 150 cm), aggressive, demersal piscivore is of considerable economic importance as a foodfish and as a quarry of sportsmen (Hart 1973). Males guard large egg masses in rocky shallow areas in winter. The larvae become neustonic; the juveniles settle in sandy areas in spring and gradually move to the deeper rocky habitat of the adults. Larvae have been collected in several plankton surveys within the species' range and they have been illustrated and described briefly (Blackburn 1973; Phillips and Barraclough 1977). They are described here in more detail based on laboratory-reared hatchlings and a developmental series of plankton-collected specimens collected mainly off California. Larger pelagic specimens (30-52 mm) collected off southern British Columbia were also examined.

Pigmentation—At hatching (9.3 mm) the larval pigment pattern is already established (Fig. 4). The overall appearance is of a heavily, uniformly pigmented larva with unpigmented finfolds and an unpigmented caudal region. The optic lobes of the brain are densely covered with melanophores. Some spots are also present on the olfactory lobes and between the nares. The hindbrain is covered with a medial patch of pigment that divides into two lines that straddle the middorsal septum reaching posterior to above the end of the gut. At that point they join and run along the middorsal septum for most of the rest of the length of the body. Pigment extends onto the flank

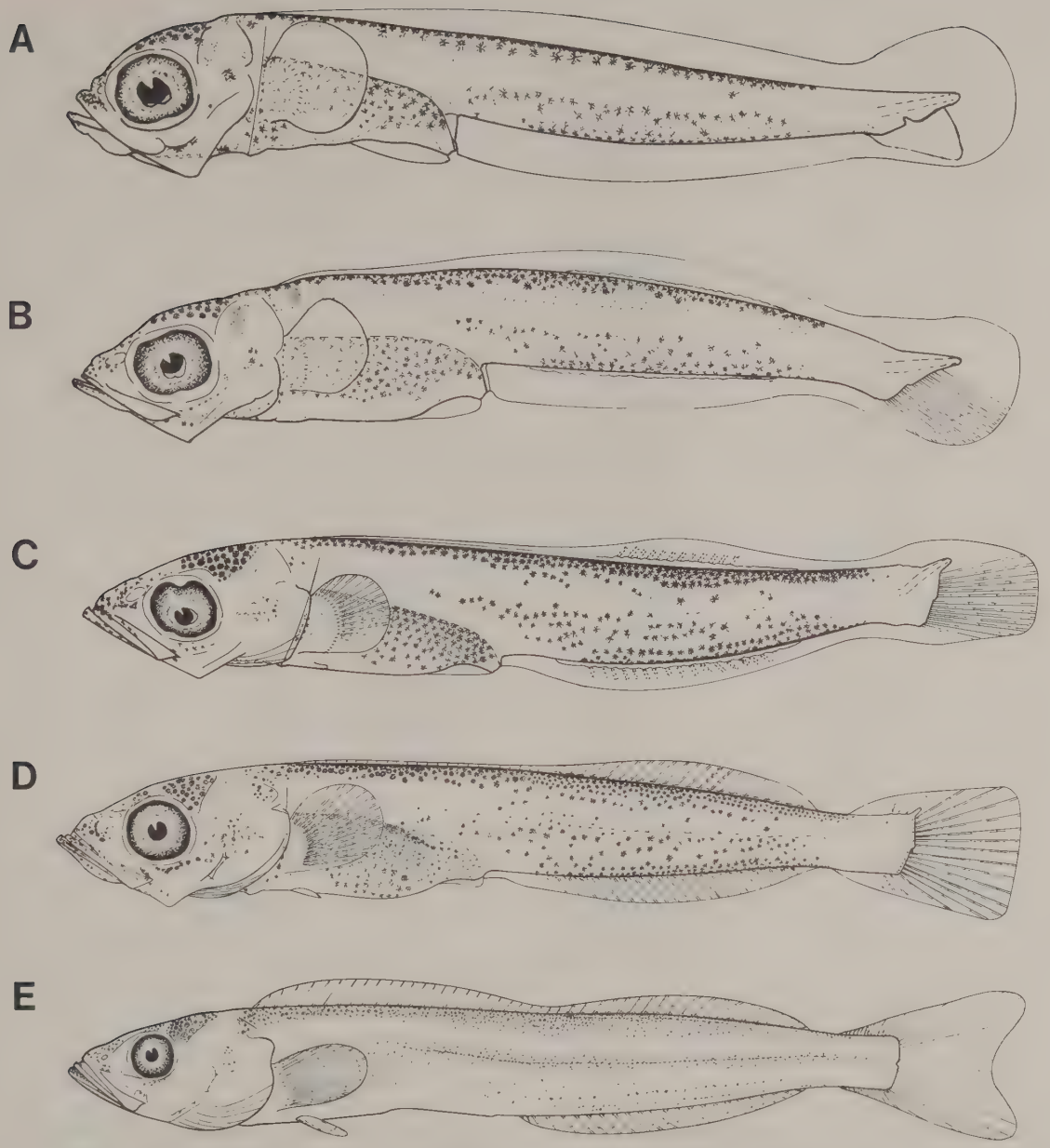

Figure 4.—Larvae of *Ophiodon elongatus*: A. 9.8 mm, B. 12.2 mm, C. 15.4 mm, D. 19.0 mm, E. 36.0 mm.

of the trunk and joins more closely spaced melanophores that extend dorsally from a line along the midventral septum. The midventral pigment line originates about six myomeres posterior to the anus and does not extend posteriorly quite as far as the dorsal line. Dorsolaterally the peritoneum is covered with melanophores, and there is a spot in the opercular region on some specimens. The base of the isthmus may have a melanophore. As the larvae grow, pigment is added to certain parts of the pattern seen in the hatchlings; the most significant changes occur in the head region. By 12 mm there are pigment spots on the jaws, in the suborbital, opercular, and cleithral areas, and the isthmus is densely pigmented. More of the lateral surface of the peritoneum is pigmented, and the trunk flank pigment extends forward to the gut. To a variable extent there is an indication of a line of fine pigment spots along the midlateral septum that increases in intensity with growth. The dorsal line of pigment spots straddles the middorsal septum for nearly all of its length—coincident with the base of the dorsal fin. Internally there is heavy pigment along the vertebral column medially just dorsal and ventral to the vertebrae. None of the fins

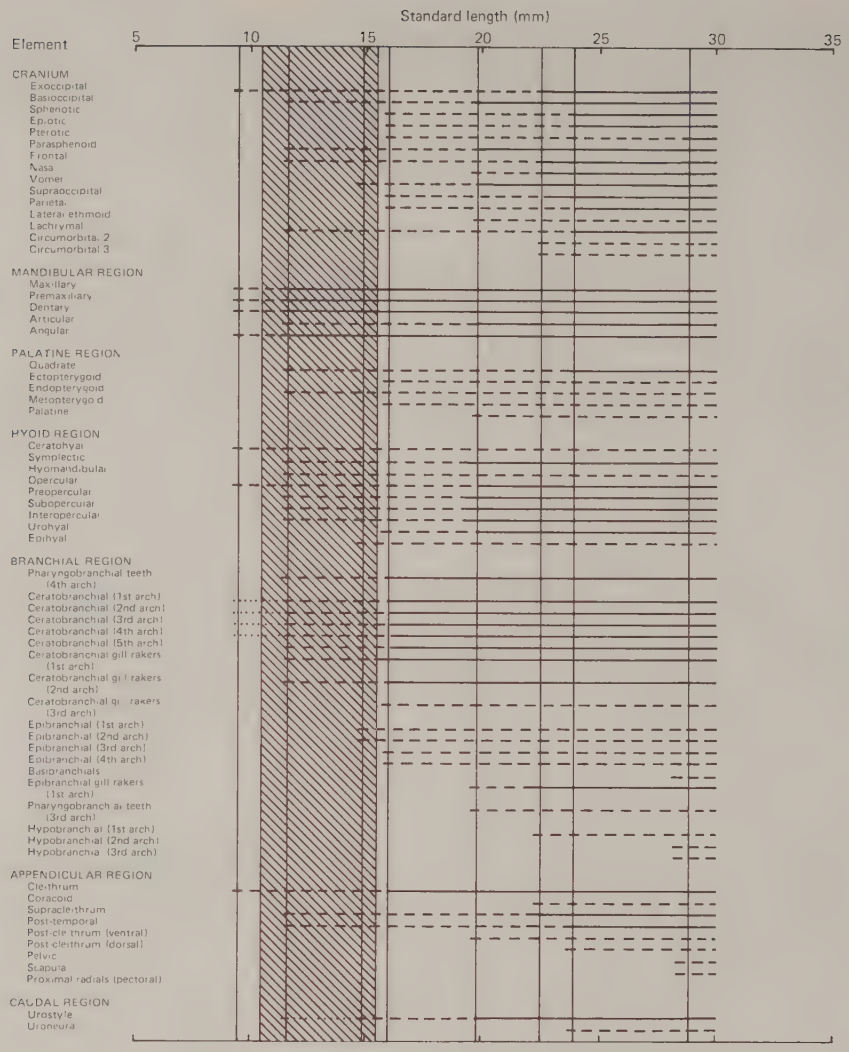

Figure 5.—Ossification of major bones in *Ophiodon elongatus*. Symbols as in Figure 2.

develop pigment during the larval stage. There is remarkably little change in pigmentation from the 12 mm larva to the largest specimen on hand (52 mm).

Morphology—A series of 83 specimens 9.0-52.0 mm was measured to document body shape which changes little during development. The larvae are elongate, have long pointed snouts with large mouths, and a long gut. The lower jaw protrudes noticeably in larvae > 12 mm. Notochord flexion occurs in larvae 11-15 mm. There is a preanal finfold throughout the larval period. Two small blunt spines occur on the preopercular margin in larvae > 18 mm and four spines are present in 40 mm fish. There is no marked transformation from larvae to juveniles in *O. elongatus* and the fish seem to remain epipelagic until well after the larval period, which ends at about 30 mm.

Developmental Osteology—A series of 30 larvae from 9.5 to 28.9 mm and a 40.0 mm specimen were cleared and stained to trace osteological development (Table 4). Meristic elements develop over a wide length range: The branchiostegal rays had started to ossify on the smallest specimen examined, but the pelvic fins, gill rakers, and secondary caudal rays had not reached their adult complements on a 28.9 mm specimen. Elements in most meristic features start to ossify during flexion (10.5-15.5 mm). The vertebrae form from anterior to posterior, except that the urostyle is among the first centra to form.

Nonmeristic bones that have started to ossify in the smallest specimens examined include the cleithrum, opercle, maxillary, premaxillary, angular, and dentary (Fig. 5). During flexion, several bones in the head region start to ossify. No early development of the posterior coracoid process in cartilage is seen; in contrast to its prominent development in some other hexagrammid larvae (*Hexagrammos lagocephalus*, *H. octogrammus*, and *Pleurogrammus monopterygius*). Also in *O. elongatus*, the bones of the jaw, which reach adult shape dur-

Table 4.—Development of meristic structures of *Ophiodon elongatus*. Specimens between dashed lines are undergoing notochord flexion. The first observation of count within adult range is underlined.

Standard length (mm)	Vertebrae[1]				Fins									Branchiostegal rays	Gill rakers	
	Precaudal		Caudal		Dorsal					Caudal						
										Upper		Lower				
	Partial	Complete	Partial	Complete	First	Second	Anal	Pectoral	Pelvic	Secondary	Principal	Principal	Secondary		Upper	Lower
9.5														2		
9.5														2		
10.4								3			3	3		3		
10.5								5			3	3		4		
11.2								8			7	7		5		6
11.7								8			7	7		5		8
12.5								5			6	6		5		4
12.5								6			6	7		5		5
12.5								7			6	7		5		7
13.5	3							8			7	7		5		8
13.5								8			6	7		6		8
13.5	2	2		1				9		1	7	7	1	6		9
13.5	2	4		1				8			7	7	1	6		9
14.0	4							9			7	7	1	6		7
14.8	16	7	23	1				10		2	7	7	1	6		10
15.0	17	6	23					11		damaged	damaged	7	1	6		10
15.5	16	7	26	1				12		2	7	7	2	6		14
16.0	17	6	25	1				11		1	7	7	1	6		12
16.2	13	9	28	1		16	17	13		3	7	7	3	6	1	13
17.5	13	9	30	1		18	19	14		4	7	7	3	6	1	13
17.5	11	13	31	1	5	18	19	14		4	7	7	3	7	1	13
17.5	3	21	32	1	8	18	20	14		4	7	7	3	6	1	11
18.2		23	15	18	11	19	18	15		5	7	7	4	6	1	11
18.3		23	7	26	12	19	21	15		5	7	7	4	6	1	14
19.8		23	2	31	16	20	22	16		6	7	7	5	6	2	16
21.3		24	1	32	25	21	23	17	1,3	7	7	7	7	7	2	14
22.0		23	2	32	25	21	24	17	1,3	7	7	7	6	6	2	16
22.5		23		33	25	22	24	17	1,3	8	7	7	7	6	3	17
24.0		23		32	25	21	23	18	1,4	9	7	7	8	6	3	17
28.9		24		34	27	21	25	17	1,4	9	7	7	8	6	2	14

[1]Vertebrae in hexagrammids begin ossification as dorsal and ventral saddle-shaped pieces of bone which join each other laterally to form rings that further ossify to attain their definitive shape. Vertebrae were considered "partial" if ossification had begun, but the dorsal and ventral sections had not fused, after which a vertebra was considered "complete."

ing flexion, and the ceratobranchials, which reach it shortly after flexion, are precocious relative to their development in other hexagrammids. Shortly after flexion, at about 17 mm, most of the skeletal elements are partially ossified, and the cleithrum reaches its adult shape. Most bones of the hyoid arch attain their adult shapes at about 20 mm, and most of the bones of the pectoral girdle have started to ossify by about 24 mm. The caudal skeleton begins to ossify at about 14 mm; during flexion and by the end of flexion the urostyle and four plates that support the principal caudal rays are seen: Two hypurals that support the dorsal principal caudal rays, a large hypural (hypurals 1 and 2), and the parhypural that support the ventral caudal rays. By 28.9 mm three epurals (the anterior two are ossified) and a pair of tiny uroneurals are present and the dorsal hypurals (3 and 4) have fused into one plate. The posterior epural is ossified by 40 mm. Hypural 5 is absent.

Hexagrammos Species
Figures 6-14

Larval development of the four northeastern Pacific species of *Hexagrammos* is similar to that of the northwestern Pacific species, *H. otakii* (Gorbunova 1962) and *H. agrammus* (Fukuhara 1971). Therefore a general description of larvae of the northeastern Pacific species of *Hexagrammos* will be given, followed by information to distinguish these species. Specific identity of larvae was established by comparing pigmentation on smaller larvae with that on larger larvae and prejuveniles that had distinguishing meristic characters (Table 5). Identity of field-caught *H. decagrammos* and *H. stelleri* larvae was confirmed by comparisons with larvae reared from known parents.

Pigmentation (Table 6, Figure 6)—In preflexion larvae the typical hexagrammine (*Hexagrammos* and *Pleurogrammus*) heavy pigment pattern is evident, and additional pigment appears during development. The snout, lower jaw, and dorsal surfaces of the optic lobes are covered with numerous melanophores. The isthmus and gill filaments may have a few pigment spots. A few spots are present in the cheek and opercular area, and a melanophore may be present on each angular. Two lines of pigment spots run along the dorsal midline from the optic lobe pigment to near the tip of the notochord. These lines join each other across the dorsal midline on the caudal peduncle, and to some extent along the area where the dorsal fin forms.

Table 5.—Guide for identifying northeast Pacific species of *Hexagrammos* based on meristic characters.

Based on principal ventral caudal fin rays	
Principal ventral caudal rays = 8	
precaudal vertebrae = 20-22	*H. stelleri*
precaudal vertebrae = 18-19	*H. octogrammus*
Principal ventral caudal rays = 9	*H. decagrammus*
Principal ventral caudal rays = 10	*H. lagocephalus*
Based on extremes of meristic characters	
Dorsal fin spinous rays	
18-19	*H. octogrammus*
20-23	indeterminate
24-25	*H. stelleri*
Dorsal fin softrays	
18-19	*H. stelleri*
20-25	indeterminate
26	*H. decagrammus*
Total anal fin rays	
21	*H. lagocephalus*
22-26	indeterminate
Precaudal vertebrae	
18-19	*H. octogrammus*
20-23	indeterminate
Caudal vertebrae	
31	*H. stelleri*
32-35	indeterminate
Total vertebrae	
50	*H. octogrammus*
51-57	indeterminate

The dorsolateral surface of the peritoneum is pigmented. The flank is variably pigmented with internal and superficial pigment spots dorsal and ventral to the notochord. Deep internal pigment is present just dorsal and ventral to the developing vertebral column. Ventral midline pigment is present in preflexion larvae of some species but is present only later in development in other species. This pigment consists of a row of pigment spots along each side of the area where the base of the anal fin forms and extends onto the caudal peduncle where it is intensified in some species. The tip of the notochord has a line of a few melanophores along its dorsal surface in some species.

As the larvae grow, the most conspicuous area of added pigment is the flank where both superficial and internal spots eventually cover the entire lateral surface of the body giving the fish a uniformly dark appearance. The caudal fin rays and fin membrane become pigmented as they develop, particularly at their bases. The peritoneal pigment extends ventrally to cover the gut cavity.

Morphology—*Hexagrammos* larvae hatch at between 7 and 9 mm and notochord flexion occurs between 12 and 18 mm. No remarkable changes in body shape occur during development (Appendix Figures 1-10). *Hexagrammos* larvae have blunt heads with large eyes and small subterminal or upturned mouths. The body is elongate and tubular. The gut is short and compact. Among the four species of *Hexagrammos* studied here, *H. lagocephalus* is deeper bodied at the pectoral fin and at the caudal peduncle than the others. There is no marked transformation at the end of the larval period, rather the fish remain epipelagic until about 40-50 mm, when they become demersal and develop pigmentation and body shape characteristic of the adults.

Developmental Osteology (Tables 7-10)—Examination of cleared and stained developmental series of each species of *Hexagrammos* showed that the sequence of formation and ossification of most bony elements follows a similar pattern among the species. Among meristic elements, branchiostegal rays are first to form, starting in preflexion larvae, and attaining adult counts during flexion. Principal caudal fin rays ossify during flexion. Secondary caudal fin rays are gradually added beginning during flexion and continuing into the prejuvenile stage. First arch gill rakers form before or during flexion and continue to form until late in the prejuvenile stage. Pectoral fin rays start to develop during flexion and adult counts are attained in the early postflexion period. Vertebral development is from anterior to posterior, with abdominal vertebrae ossifying during and shortly after flexion. The urostyle ossifies before the rest of the caudal vertebrae, which ossify late in the flexion stage and complete development rapidly. Several vertebrae are in various stages of development on each flexion and early postflexion larva. The second dorsal and anal fin rays develop rapidly shortly after flexion, followed by the first dorsal fin spines and finally the pelvic fin rays which do not form until early in the prejuvenile stage.

Evidence of the beginning of development of the caudal complex is first seen concurrent with the start of flexion when the principal caudal fin rays start to form. At this time the hypurals start to develop as cartilage. Posteriorly a medially bifurcated cartilaginous wedge is seen representing the dorsal hypural plate (hypurals 3 and 4). Anterior to this a trapezoidal shaped piece of cartilage with two openings represents the ventral hypural plate (parhypural and hypurals 1 and 2). Later during the flexion period the three epurals develop from cartilage followed by a single thin pair of bony uroneurals. The urostyle is the first structure to ossify followed by the hypural plates, the uroneurals, and the epurals. A shortened neural spine is present on the urostyle and on preural centrum 2 the neural spine is shortened and is double in some individuals. The hemal spines on the first two preural centra are autogenous. The principal caudal fin ray count is 7 dorsal and 8 to 10 ventral, depending on the species (*H. stelleri* and *H. octogrammus*: 8; *H. decagrammus*: 9; *H. lagocephalus*: 10). Dorsal and ventral secondary caudal fin rays are numerous (12-19).

The sequence of ossification of bones in the species of *Hexagrammos* examined follows a fairly constant pattern (Figs. 8, 10, 12, 14). The first bone to ossify is the cleithrum, which is present at hatching. The bones associated with the mouth (maxillary, dentary, and premaxillary) ossify before flexion. The exoccipital at the base of the skull; the quadrate, symplectic, and hyomandibular of the suspensorium; ceratohyal and epihyal and the ceratobranchials of the branchial apparatus; the pharyngobranchial teeth; and an elongate posterior coracoid process form as cartilage in preflexion larvae.

During flexion, in the skull the parasphenoid and exoccipital start to ossify and more of the occipital bones and bones of the otic region are present as cartilage. The rest of the bones of the mandibular arch, those in the opercular series, the ceratobranchials, and the supracleithrum and posttemporal also start to ossify. Shortly after flexion is complete, most of the bones

Table 6.—Pigmentation characteristics that distinguish larvae (<30 mm; >25 mm meristic characters permit separation) of the four species of *Hexagrammos* in the northeast Pacific. Considerable individual variation in number, position, and degree of contraction of melanophores (spots) was observed; the modal conditions for the species are noted here so individuals may not display all characteristics mentioned.

	Pigment area						
Species	Postanal ventral midline	Superficial lateral trunk[1]	Isthmus	Notochord tip	Gular[2]	Internal pectoral fin base[3] (>17 mm)	Other
H. stelleri	Absent until about 15 mm, then starts to form posteriorly (on caudal peduncle), later (~23mm) forms along entire base of anal fin.	Absent or faint until 9 mm. Then ventral row densest. Concentrated above and below lateral midline.	Absent at hatching. Anterior half gradually becomes pigmented starting at 10 mm.	Absent	Absent	Present	Lower jaw pigment on tip only.
H. decagrammus	Absent until about 13 mm, then starts to form along anal fin base near its origin. By 18 mm along anal fin base to caudal peduncle. Spots more numerous and smaller than on *H. lagocephalus*.	Some present at hatching (~8 mm). Ventral row densest. Longer, denser, and broader than on *H. stelleri*.	About four equal sized and spaced spots form on each side making a "V." Present from about 9 mm on.	Absent at hatching but forms by about 10 mm.	Present >12 mm	Inconsistently present	Two forms based on degree of contraction of melanophores, particularly the lateral trunk ones.
H. lagocephalus	Present throughout development. Particularly dense on caudal peduncle. Spots along anal fin base tend not to touch each other. Spots uneven in spacing and size to create irregular line. Few spots anterior to origin of anal fin.	Faint at hatching (~8 mm). Ventral row of more smaller spots than in *H. stelleri* or *H. decagrammus*. Posterior part of dorsal row nearly as dense as ventral row at <15 mm, then uniform.	An anterior medial spot and about five equal sized and spaced spots present from about 9 mm on.	Present	Present >11 mm	Absent	Tends to be clear area between optic lobes.
H. octogrammus	Present throughout development. Extends from anus to base of caudal fin. Dense on caudal peduncle. Spots tend to touch each other to create a continuous straight line.	Absent or faint at hatching (~7 mm). Denser on caudal peduncle than anteriorly. Spots smaller than on *H. stelleri* or *H. decagrammus* but larger than on *H. lagocephalus*.	Present— anteriormost and posteriormost spots larger than others. Anterior, medial spot seen at 10 mm, up to five on each side of isthmus seen at 12 mm. Spacing uneven.	Present	Absent	Present	Heavy pectoral base pigment. Pigment continuous between optic lobes.

[1]On specimens larger than about 20 mm SL the lateral aspect of the trunk is uniformly densely pigmented in all species.
[2]A few spots occur ventrally just anterior to the isthmus.
[3]One to a few spots occur near the dorsal edge of the internal surface of the pectoral fin base.

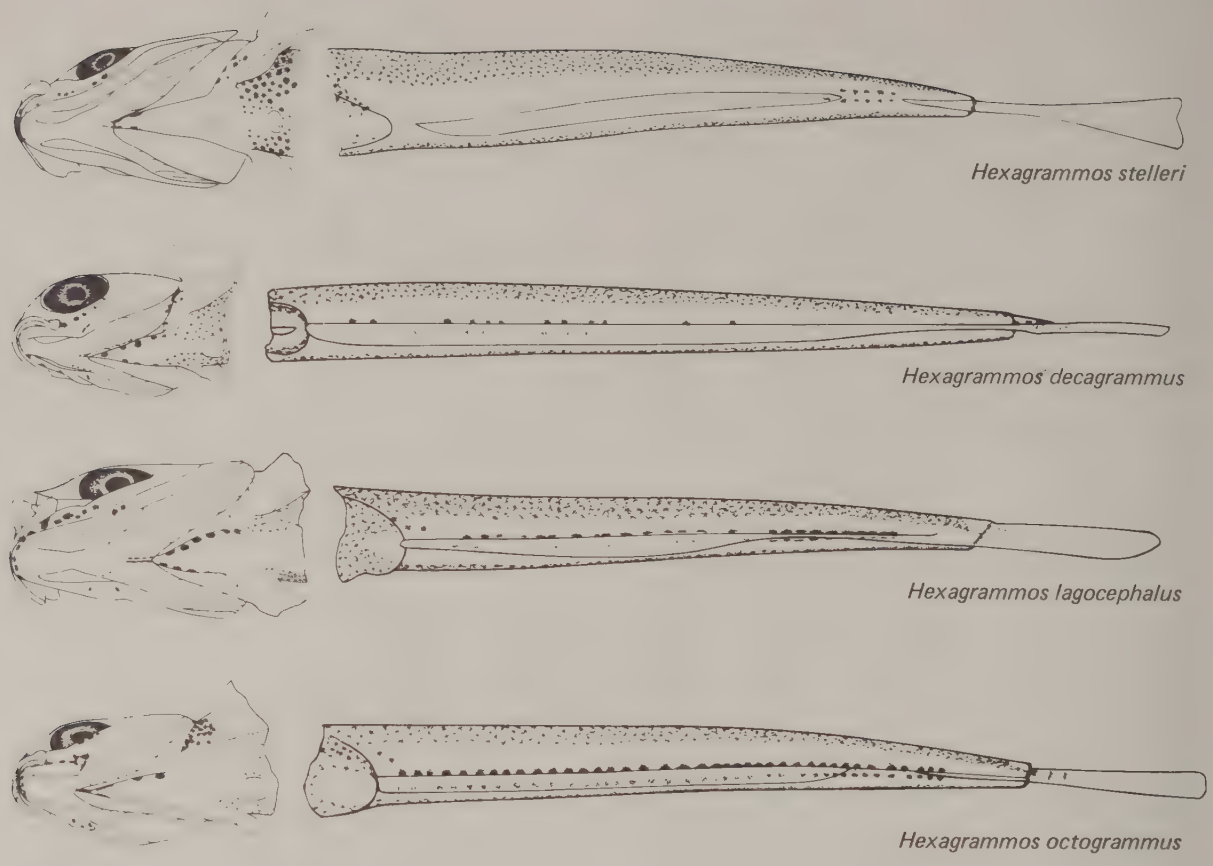

Figure 6.—Representative ventral views of head and tail regions of larvae of *Hexagrammos* (16-18 mm). A. *H. stelleri*, B. *H. decagrammus*, C. *H. lagocephalus*, D. *H. octogrammus*.

of the skull are visible, either as cartilage or bone. The bones of the jaws and those of the opercular series assume their adult shapes.

During the postflexion period, most of the rest of the bones start to ossify, and the entire skeleton approaches its adult appearance. Late-forming bones include circumorbitals, palatine, basibranchials, hypobranchials, and proximal radials of the pectoral fin.

Hexagrammos stelleri (Whitespotted Greenling) Figures 6, 7, and 8

This greenling occurs in rocky coastal areas from Washington to northern Japan (Quast 1960). Spawning of blue demersal eggs is reported to occur during every season (Gorbunova 1962; Hart 1973). Larvae were illustrated and described by Gorbunova (1962).

The larvae illustrated here were reared from eggs found in Puget Sound. Similar larvae from plankton collections in the Gulf of Alaska were used for morphometric and osteological observations.

Larvae of *H. stelleri* are the least pigmented larvae in the genus (Table 6). Postanal ventral midline pigment is absent until about 15 mm, when it starts to form on the caudal peduncle and at about 23 mm forms along the anal fin base. Superficial lateral trunk pigment is absent or faint until the larvae reach about 9 mm, then the ventral aspect is more densely pigmented than the dorsal aspect. The isthmus is pigmented anteriorly in larvae larger than 10 mm. Only the tip of the lower jaw and the angular are pigmented, while the entire lower jaw is pigmented in the three other species.

Hexagrammos decagrammus (Kelp Greenling) Figures 6, 9, and 10

The geographic range of the rather abundant kelp greenling is extensive—from the Aleutians to southern California (Miller and Lea 1972). Large masses of pale blue eggs are laid in the fall (Hart 1973) off British Columbia and in late summer to the north (Gorbunova 1962). Larval development was described by Gorbunova (1962) under the name *H. superciliosus*. Larvae illustrated and described here were either reared from eggs or gleaned from plankton samples. Specimens from off California were about 2 mm shorter at comparable stages of development than those off Alaska. The sizes reported here apply to the larvae from Alaska.

On hatching at about 8.0 mm *H. decagrammus* has no pigment along the postanal ventral midline, but there is a little

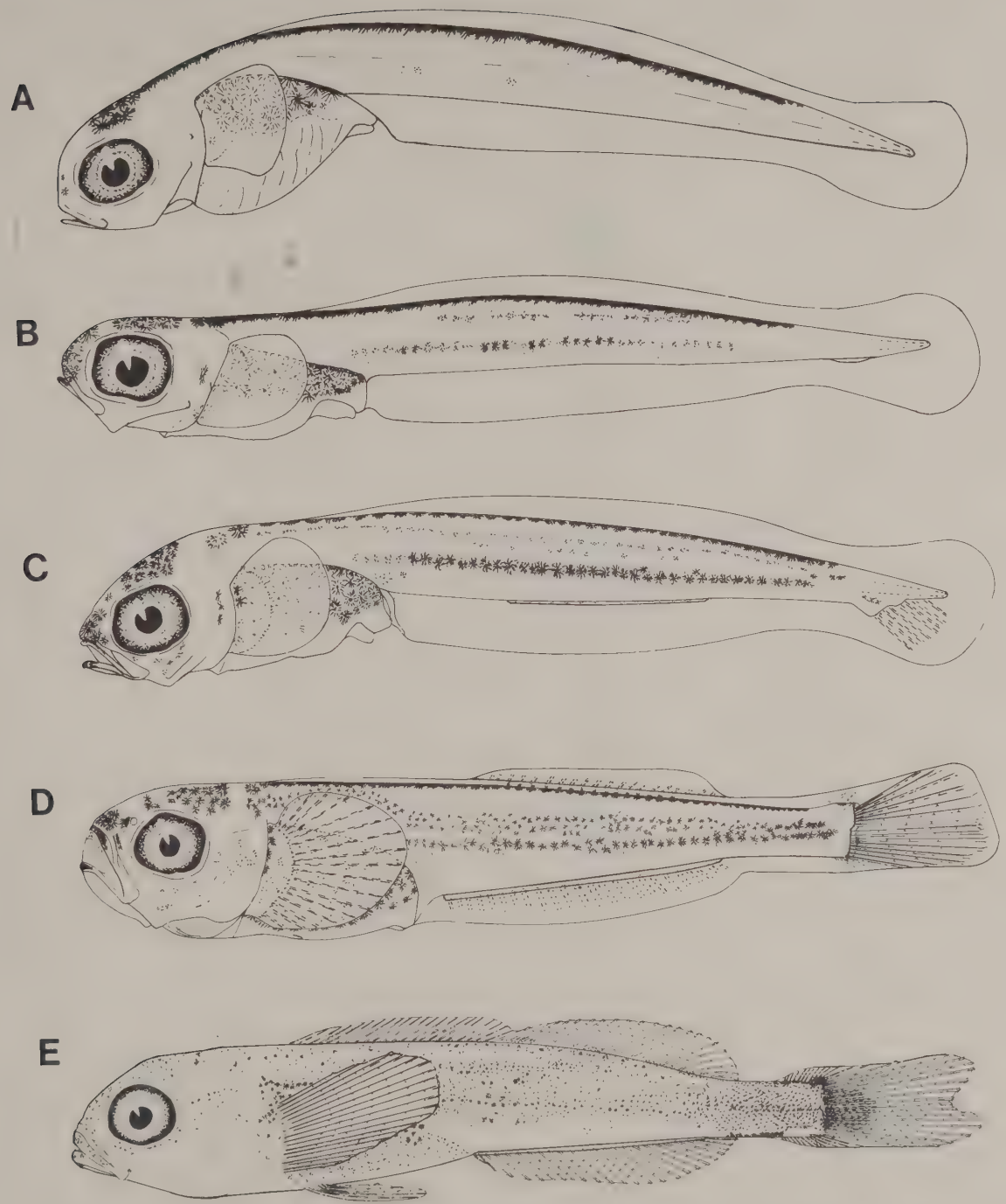

Figure 7.—Larvae of *Hexagrammos stelleri*: A. 8.0 mm, B. 9.2 mm, C. 10.4 mm, D. 13.8 mm, E. 33.0 mm.

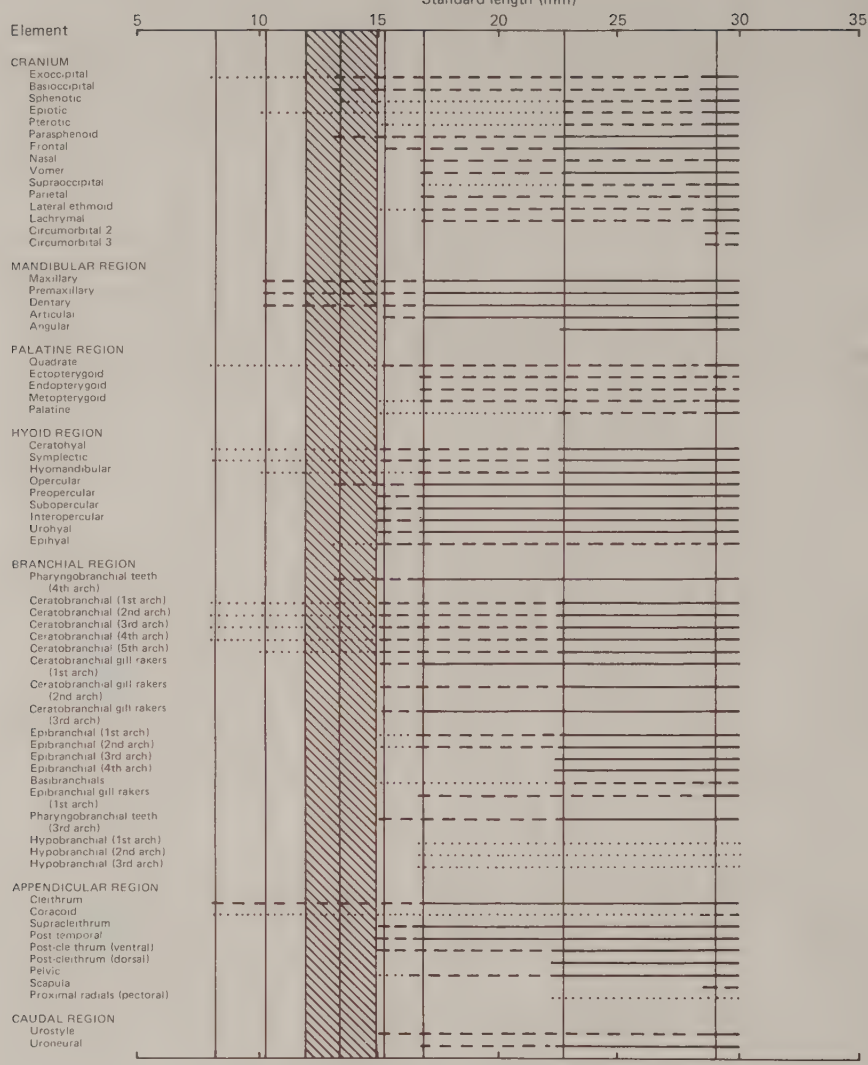

Figure 8.—Ossification of major bones in *Hexagrammos stelleri*. Symbols as in Figure 2.

Table 7.—Development of meristic structures of *Hexagrammos stelleri*. Specimens between dashed lines are undergoing notochord flexion. The first observation of count within adult range is underlined.

Standard length (mm)	Vertebrae[1]				Fins									Branchiostegal rays	Gill rakers	
	Precaudal		Caudal		Dorsal					Caudal						
										Upper		Lower				
	Partial	Complete	Partial	Complete	First	Second	Anal	Pectoral	Pelvic	Secondary	Principal	Principal	Secondary		Upper	Lower
8.3																
9.4														3		
9.6														3		
10.2														3		
10.4														3		
11.7														4		
11.7														5		2
12.4											4	4		5		3
12.6								7			4	4		5		4
13.3														5		3
13.8	20		32					11			7	8		6		6
14.6	20		30					13			7	8		6		6
14.9		20	7	27				13		2	7	8	2	6		7
15.0	15	5	31					14			7	8		6		7
15.3		20	11	22				13		2	7	8	2	6		7
15.5		21	7	25				16		3	7	8	2	6		7
15.6	2	19	28	3				14		2	7	8	2	6		8
16.8		21	4	29		20	23	18		6	7	8	6	6		8
17.1		21		33		20	23	20	1,2	8	7	8	7	6	1	9
18.5		21		33	22	21	24	19	1,4	10	7	8	10	6	1	9
18.7		21		32	21	21	23	19	1,3	8	7	8	8	6	1	11
19.7		20		34	12	20	24	20	1,3	7	7	8	9	6	2	9
20.6		20		33	24	18	24	19	1,4	damaged	7	8	10	6	2	9
20.7		21		32	22	20	22	20	1,3	10	7	8	9	6	2	9
21.9		21		32	22	20	25	20	1,4	11	7	8	11	6	2	9
21.9		20		34	23	21	26	19	1,4	10	7	8	9	6	2	10
22.9		21		32	22	21	24	20	1,5	14	7	8	13	6	2	10
22.9		21		33	23	21	25	19	1,5	15	7	8	13	6	3	10
24.1		21		33	23	22	24	19	1,5	14	7	8	14	6	3	9
29.0		21		32	23	22	24	19	1,5	17	7	8	15	6	3	10
29.6		20		32	22	21	25	20	1,5	16	7	8	15	6	4	11
34.0		21		32	23	21	25	19	1,5	18	7	8	16	6	4	12
40.6		21		33	22	22	25	20	1,5	17	7	8	15	6	3	11
44.2		20		34	24	21	25	20	1,5	19	7	8	17	6	3	12
49.5		21		33	23	21	25	19	1,5	17	7	8	16	6	3	11

[1]Vertebrae in hexagrammids begin ossification as dorsal and ventral saddle-shaped pieces of bone which join each other laterally to form rings that further ossify to attain their definitive shape. Vertebrae were considered "partial" if ossification had begun, but the dorsal and ventral sections had not fused, after which a vertebra was considered "complete."

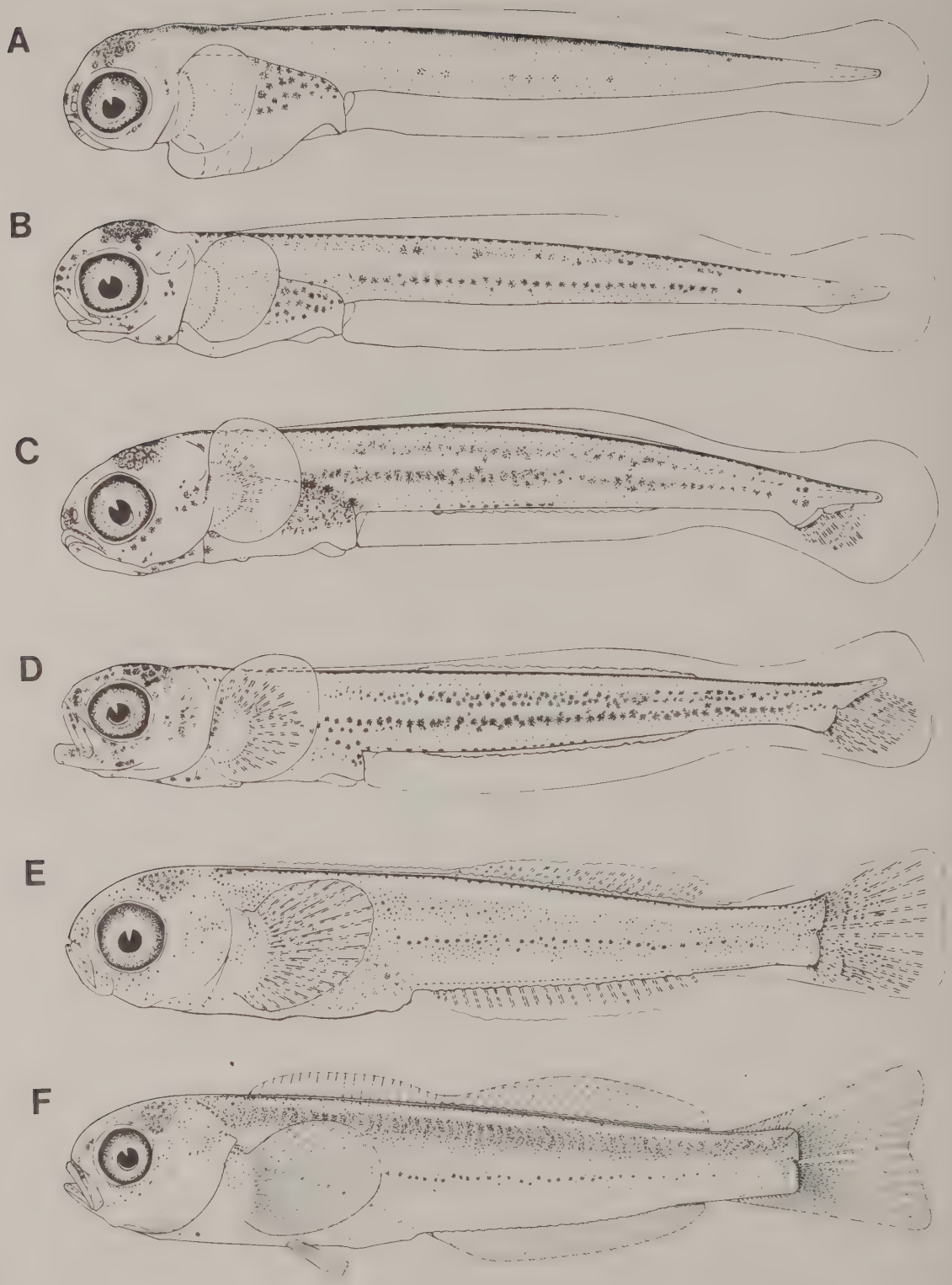

Figure 9.—Larvae of *Hexagrammos decagrammus*: A. 9.8 mm, B. 10.6 mm, C. 13.3 mm, D. 15.0 mm, E. 18.2 mm, F. 31.0 mm.

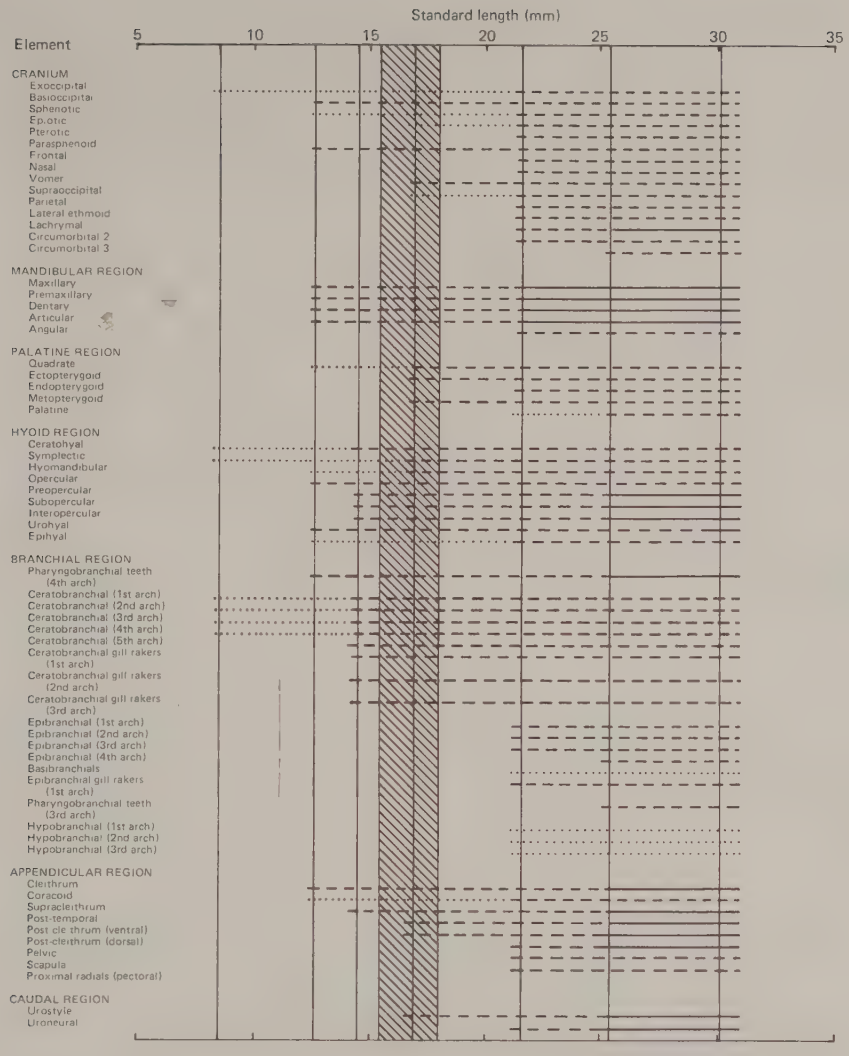

Figure 10.—Ossification of major bones in *Hexagrammos decagrammus*. Symbols as in Figure 2.

Table 8.—Development of meristic structures of *Hexagrammos decagrammus*. Specimens between dashed lines are undergoing notochord flexion. The first observation of count within adult range is underlined.

Standard length (mm)	Vertebrae[1]				Fins									Branchiostegal rays	Gill rakers	
	Precaudal		Caudal		Dorsal					Caudal						
										Upper		Lower				
	Partial	Complete	Partial	Complete	First	Second	Anal	Pectoral	Pelvic	Secondary	Principal	Principal	Secondary		Upper	Lower
12.0																
12.1														3		
12.5														2		
12.5														3		
12.7														1		
13.2														2		
14.6														4		
14.6														5	2	
15.6								8			4	5		6	2	
16.0											3	3		6	3	
16.8	16	6	31					13			7	9		6	5	
17.0	15	6	31					12			6	8		6	4	
17.4	15	6	31					10			7	9		6	6	
17.8	14	7	31					14			7	9		6	4	
17.9	13	8	32	1				15			7	9	1	6	5	
18.4	5	17	29	damaged			9	17		1	7	9	1	6	damaged	
19.4		21	24	10				19		4	7	9	3	6	7	
19.4		21	2	31			21	18		4	7	9	3	6	8	
20.2		21		35			19	18		4	7	9	3	6	8	
20.4		22		34		15	22	19	1,3	5	7	9	4	6	8	
20.6		21		35		21	22	19	1,3	5	7	9	4	6	8	
20.9		21		35		21	21	19	1,3	6	7	9	5	6	8	
21.0		21		34	13	21	24	19	1,3	7	7	9	6	6	9	
22.2		21		35		23	24	19	1,4	7	7	9	9	6	9	
22.5		21		35		22	23	19	1,4	6	7	9	5	6	9	
23.8		21		35	18	23	24	18	1,4	8	7	9	7	6	9	
23.8		21		35	18	23	25	19	1,4	8	7	9	8	6	9	
24.6		21		35	21	24	24	19	1,5	9	7	9	10	6	9	
25.6		21		35	21	25	25	19	1,5	10	7	9	10	6	9	

[1]Vertebrae in hexagrammids begin ossification as dorsal and ventral saddle-shaped pieces of bone which join each other laterally to form rings that further ossify to attain their definitive shape. Vertebrae were considered "partial" if ossification had begun, but the dorsal and ventral sections had not fused, after which a vertebra was considered "complete."

superficial trunk pigment. The superficial trunk pigment ventral to the midline is heavy throughout development, relative to the other species. The isthmus is pigmented along its length and there is some pigment on the dorsal surface of the tip of the notochord. At about 13 mm, postanal ventral midline pigment is seen as a row of melanophores starting near the origin of the anal fin, with more melanophores added posteriorly as the fish grow. Some pigment spots are also added at the base of the incipient caudal fin rays. The lateral body surface is rather heavily pigmented superficially. By 18 mm, the postanal midline melanophores extend from the anus onto the caudal peduncle, and the proximal halves of the caudal fin rays are heavily pigmented. We found two forms of *H. decagrammus* larvae depending on the degree of contraction of the melanophores, particularly those of the superficial lateral series and of the postanal ventral midline series. On some individuals these are quite expanded giving the larva a dark cast and a smudgy appearance at low magnification. On other individuals these melanophores appear much more discrete with unpigmented areas between. Sometimes both types of larvae were found in the same sample, so the differences do not seem related to time or area of capture or handling of the sample. This type of variation was not seen on the other three species considered here.

Hexagrammos lagocephalus (Rock Greenling) Figures 6, 11, and 12

There is some confusion concerning the taxonomy of this greenling, which occurs from California to Japan (Quast 1964). Quast (1960) synonomized *H. superciliosus*, the eastern form, with *H. lagocephalus*, the western form. However Harris and Hartt (1977) reported two forms of rock greenling in bays of Kodiak Island, Alaska, both of which they called *H. lagocephalus*. Miller and Lea (1972) considered the rock greenling off California distinct from that found to the west and used the name *H. superciliosus* for it following a personal communication from Hubbs and Follett. If there were one species of rock greenling it would be by far the widest ranging species in the genus. Gorbunova (1962) described larvae as *H. lagocephalus* which were collected from the Andreanof Islands west of northern Japan. These larvae are distinct from those of *H. lagocephalus* described here, that were collected primarily from the Kodiak region, in that they have more intense pigment ventrally on the caudal peduncle and the ventral midline pigment does not extend forward to the developing anal fin. No such larvae were found in our samples, taken mainly from east of long. 180°. We will use the name *H. lagocephalus* for the larvae we describe, with the understanding that if two spe-

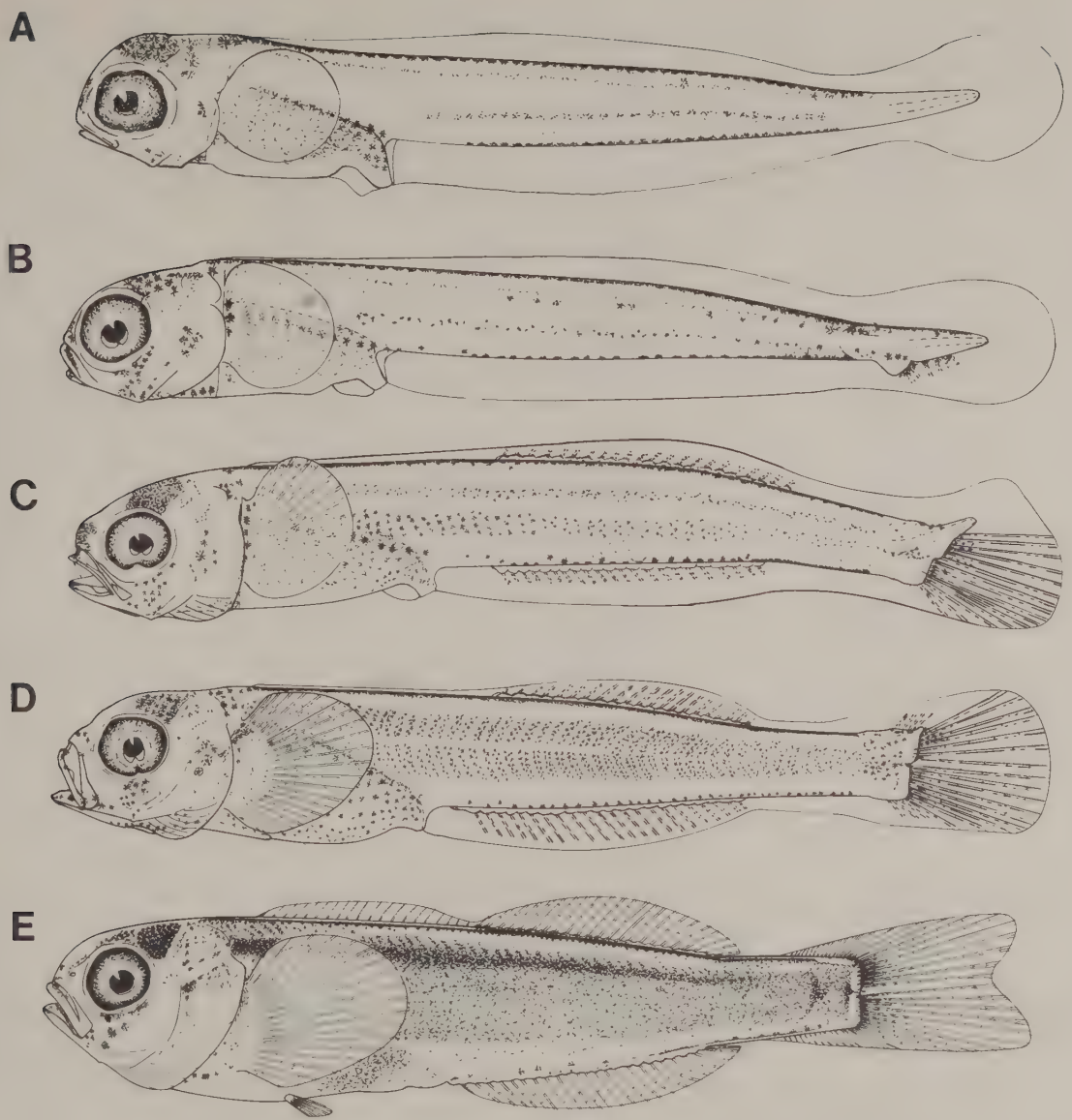

Figure 11.—Larvae of *Hexagrammos lagocephalus*: A. 8.5 mm, B. 11.2 mm, C. 14.5 mm, D. 16.8 mm, E. 28.0 mm.

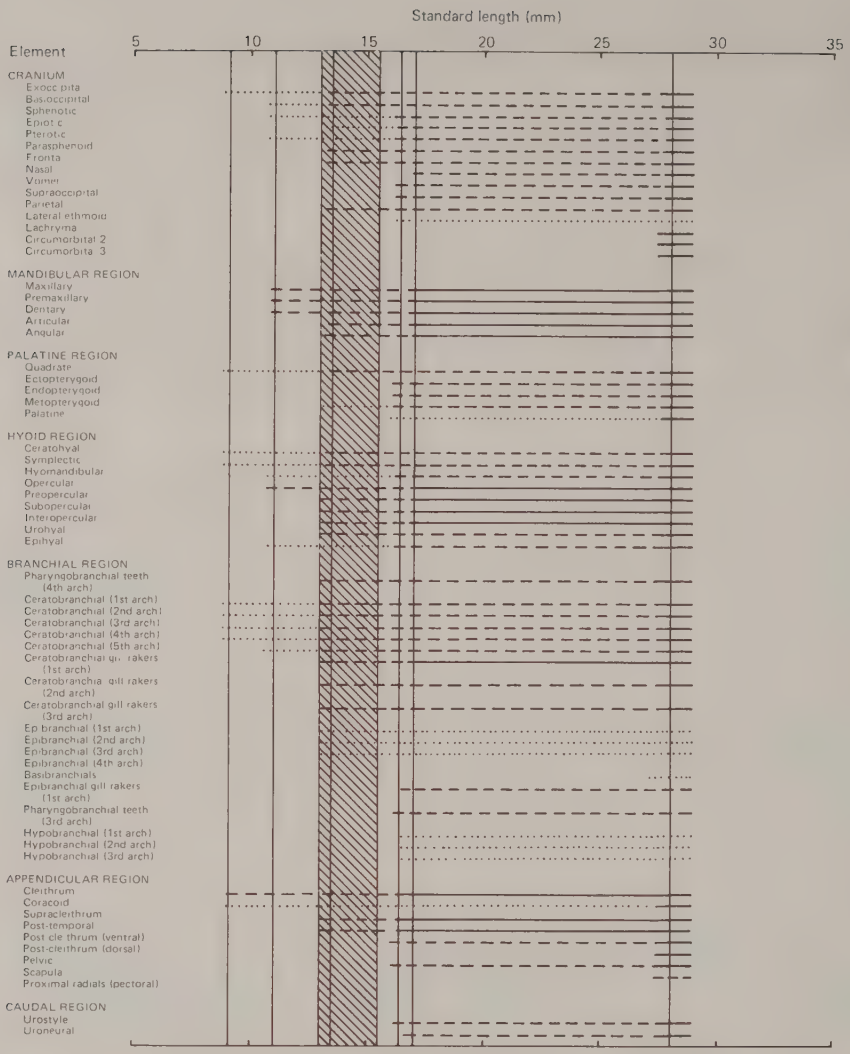

Figure 12.—Ossification of major bones in *Hexagrammos lagocephalus*. Symbols as in Figure 2.

Table 9.—Development of meristic structures of *Hexagrammos lagocephalus*. Specimens between dashed lines are undergoing notochord flexion. The first observation of count within adult range is underlined.

Standard length (mm)	Vertebrae[1]				Fins									Branchiostegal rays	Gill rakers	
	Precaudal		Caudal		Dorsal		Anal	Pectoral	Pelvic	Caudal						
										Upper		Lower				
	Partial	Complete	Partial	Complete	First	Second				Secondary	Principal	Principal	Secondary		Upper	Lower
9.9																
10.7														2		
11.0														2		
11.1														2		
11.2														4		
12.8											3	4		5		3
12.9											5	6		5		3
13.1	16	4	30					10			6	7		6		4
13.4	13	5	33					10			6	7		6		5
14.0	2							12			6	7		6		6
14.1	2										5	6		5		4
15.3	15	6	31	1		18	18	16		3	7	10	3	6		6
15.5	15	5	31	1		14	16	14			7	10	1	6		6
16.3		20	32	2		17	21	18		4	7	10	4	6		7
16.6	15	5	32	1		20	17	15		4	7	10	3	6		6
16.8		21	24	8		22	22	18		6	7	10	5	6		7
17.0		20	2	32		20	22	19		6	7	10	6	6		7
28.0		20		33	20	23	23	19	1,5	18	7	10	16	6	2	9

[1]Vertebrae in hexagrammids begin ossification as dorsal and ventral saddle-shaped pieces of bone which join each other laterally to form rings that further ossify to attain their definitive shape. Vertebrae were considered "partial" if ossification had begun, but the dorsal and ventral sections had not fused, after which a vertebra was considered "complete."

cies are again recognized these larvae would be those of *H. superciliosus.*

Gorbunova (1962) described as *H. decagrammus* larvae that we believe to be *H. lagocephalus*; we will describe them more fully here. Larvae of *H. lagocephalus* are moderately pigmented with respect to other members of the genus. Except at its anterior and posterior extremes, the postanal ventral midline is pigmented throughout development, and the pigment is particularly dense along the caudal peduncle. The pigment spots remain distinct, not touching each other. They are uneven in size and spacing and thus create an irregular line.

The ventral part of the superficial lateral trunk pigment appears darker than the dorsal part except posteriorly where the parts seem equally dark. The isthmus has about 10 evenly sized and spaced pigment spots in fish > 9 mm that create a "V" pointed anteriorly. The gular area has a few pigment spots also. The pigment covering the dorsal surface of the midbrain and hindbrain tends not to cross the dorsal midline, thus leaving a clear area between the brain hemispheres. Larvae of *H. lagocephalus* are slightly deeper bodied both at the pectoral fin base and at the caudal peduncle than other species in the genus. Since *H. lagocephalus* larvae larger than 20 mm were rare in our extensive plankton and neuston collections from the major part of the species range, this species may become demersal at a smaller size than other species of the genus which were present primarily in the neuston samples at sizes up to 40-50 mm.

Hexagrammos octogrammus (Masked Greenling) Figures 6, 13, and 14

This is the most common greenling in the Bering Sea and its geographic distribution extends south from there to off northern Japan in the west and to off northern British Columbia in the east (Rutenberg 1962; Hart 1973). It is the smallest member of the genus; Gorbunova (1962) described the early life history stages of this species. Comparable stages of development of *H. octogrammus* are attained at a slightly smaller size than the other species in the genus, although Gorbunova (1962) noted that specimens from the northern part of the range are larger at equivalent stages of development than those from the south. The smallest specimens we examined from near Kodiak Island, Alaska, were 7.0 mm.

Larvae of *H. octogrammus* are the most heavily pigmented larvae in the genus. The postanal ventral midline is pigmented along its entire length throughout development. The individual pigment spots in the line tend to touch each other making a continuous straight line. The lateral aspect of the trunk becomes densely pigmented during development, as it does in the other members of the genus. The isthmus is pigmented with about 10 spots making a "V." The melanophores are unevenly spaced and the anteriormost and posteriormost tend to be larger than the others. Pigment is present on the notochord tip and the internal surface of the pectoral fin base is heavily pigmented. The pigment that covers the midbrain and hindbrain tends to be continuous across the dorsal midline.

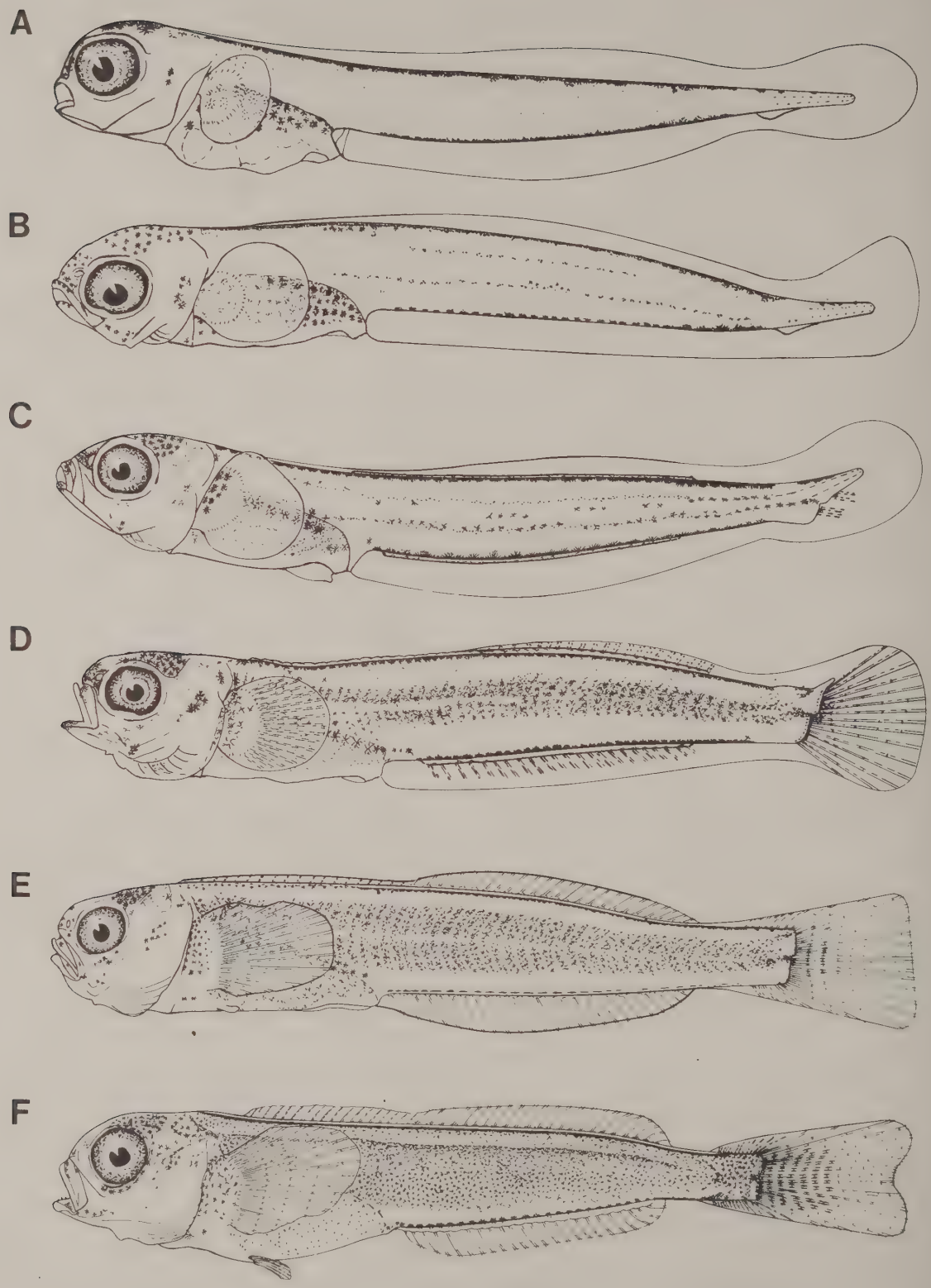

Figure 13.—Larvae of *Hexagrammos octogrammus*: A. 7.0 mm, B. 9.7 mm, C. 11.8 mm, D. 15.2 mm, E. 20.0 mm, F. 27.8 mm.

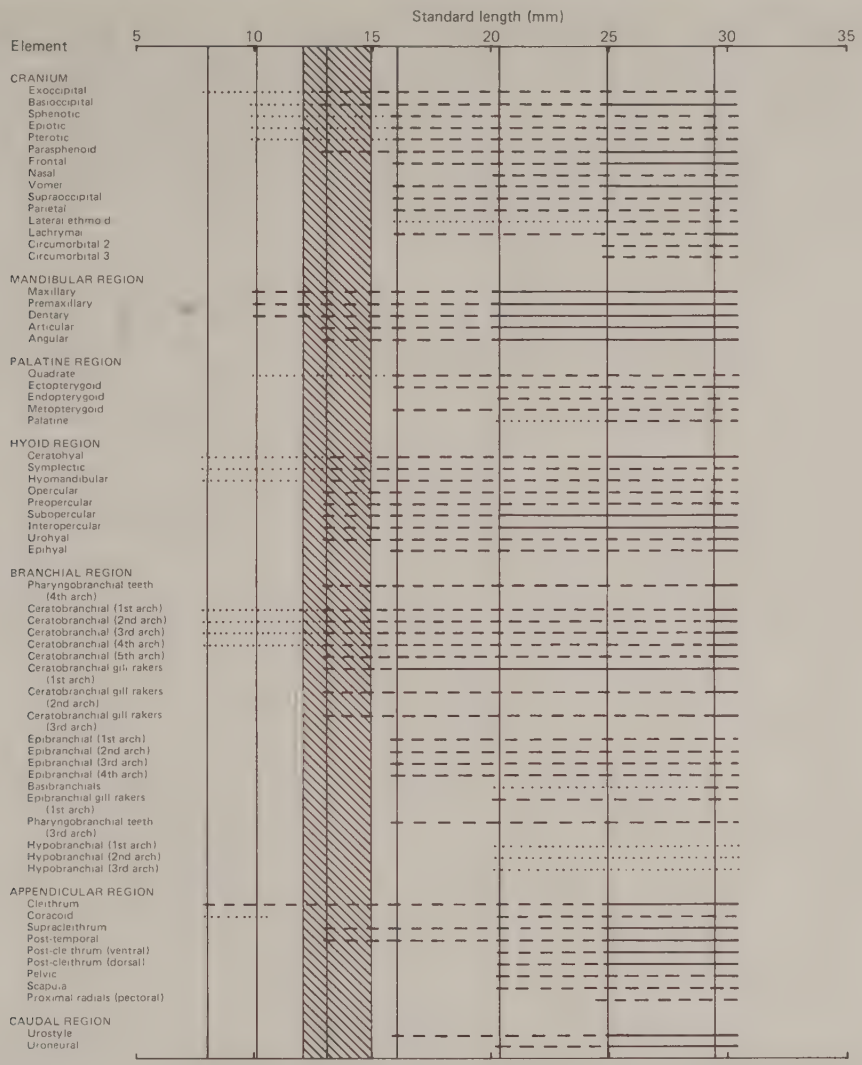

Figure 14.—Ossification of major bones in *Hexagrammos octogrammus*. Symbols as in Figure 2.

Table 10.—Development of meristic structures of *Hexagrammos octogrammus*. Specimens between dashed lines are undergoing notochord flexion. The first observation of count within adult range is underlined.

Standard length (mm)	Vertebrae[1]				Fins									Branchiostegal rays	Gill rakers	
	Precaudal		Caudal		Dorsal					Caudal						
										Upper		Lower				
	Partial	Complete	Partial	Complete	First	Second	Anal	Pectoral	Pelvic	Secondary	Principal	Principal	Secondary		Upper	Lower
8.0																
8.2														1		
8.5														1		
9.0														2		
9.5														3		
9.8														3		
10.1														4		
11.5																
11.9														5		
12.0														5		2
12.5	9		22					9			6	6		5		3
13.1	13		30					9			4	4		5		3
13.4	5	13	28	2				10			6	6		6		4
14.0		19	4	28				15		2	7	8	1	6		6
14.0		18	6	25				12			7	8		6		6
14.1		18	6	25				11			7	8		6		6
14.9		18	5	28				15		2	7	8	2	6		8
16.0		18	1	32				13		2	7	8	2	6		8
16.5		18		33				17		4	7	8	4	6		8
17.3		19		33		13	21	17		4	7	8	4	6	1	9
17.7		19		33		21	23	19		6	7	8	5	6	1	9
18.0		18		34		23	24	18		7	7	8	7	6	1	9
18.0		18		34		24	25	19		8	7	8	7	6	1	9
19.0		19		33	15	23	22	19		8	7	8	7	6		8
19.0		18		34	15	23	24	19		9	7	8	7	6		8
19.2		18		33	12	24	24	19		8	7	8	7	6		8
20.4		18		34	16	24	25	19	1,2	8	7	8	8	6	2	9
21.0		18		34	17	24	25	18	1,4	12	7	8	10	6	1	9
22.8		18		33	18	23	25	18	1,5	14	7	8	12	6	2	10
23.0		18		34	17	23	25	18	1,5	14	7	8	12	6	2	9
25.0		18		34	18	24	26	18	1,5	15	7	8	12	6	2	9
27.0		18		34	18	24	25	19	1,5	16	7	8	14	6	3	11
29.5		19		33	20	22	24	19	1,5	16	7	8	15	6	3	9
35.0		19		34	19	24	24	19	1,5	17	7	8	16	6	3	11
42.0		18		33	19	23	25	18	1,5	17	7	8	15	6	3	9
45.0		18		33	19	23	24	19	1,5	18	7	8	15	6	4	10

[1]Vertebrae in hexagrammids begin ossification as dorsal and ventral saddle-shaped pieces of bone which join each other laterally to form rings that further ossify to attain their definitive shape. Vertebrae were considered "partial" if ossification had begun, but the dorsal and ventral sections had not fused, after which a vertebra was considered "complete."

Pleurogrammus monopterygius (Atka Mackerel, Hokke) Figures 15 and 16, Appendix Figures 1-10

Following Quast (1960) only one species of *Pleurogrammus* is recognized (*P. monopterygius*) although specimens from the northwestern Pacific are often considered a separate species (*P. azonus*) (Rutenberg 1962). This species occurs in waters around the Pacific rim north of about lat. 35°N. It is fished primarily by the Republic of Korea, Japan, and the U.S.S.R.; in 1980 the catch in the United States fishery conservation zone was 33,387 t (U.S. Department of Commerce 1981). In Japan the annual catch varies from about 80 to 180 thousand t (Yusa et al. 1977). In contrast to the rest of the hexagrammines, this is a schooling pelagic fish that is reported to migrate to rocky shore areas to spawn. Spawning is reported off the Aleutian Islands in early summer (Gorbunova 1962), and off Hokkaido, Japan, in the fall (Yusa et al. 1977). The larvae and juveniles are epipelagic and are collected up to 925 km from the coast (Kobayashi 1958). Quast (1960) considered *P. monopterygius* paedomorphic and the pelagic habits of the adults can be thought of as retentions of the prejuvenile habits seen in other hexagrammines.

Early life history stages of *Pleurogrammus* under both specific names (*P. azonus* and *P. monopterygius*) have been described and illustrated several times by Japanese and Soviet authors from reared and wild caught material (Kobayashi 1958; Gorbunova 1962; Hattori 1964; Yusa 1967). Gorbunova (1962) compared larvae she considered to belong to the two species but did not report any distinguishing features of structure or pigmentation. They were separated chiefly by location of capture, with *P. azonus* larvae found west of about long. 150°E and *P. monopterygius* east of there. The larvae are similar to those of *Hexagrammos* spp. and can be distinguished

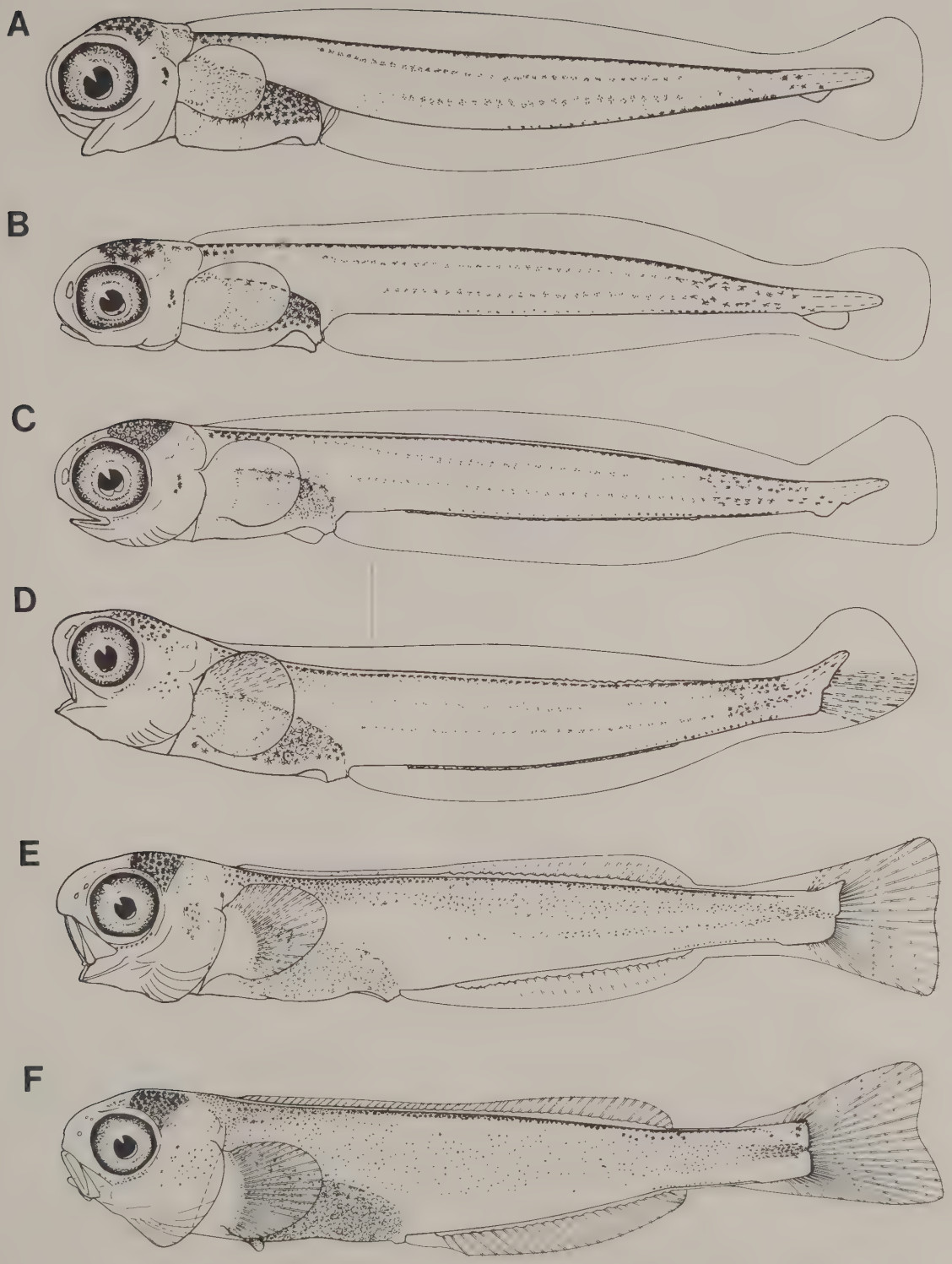

Figure 15.—Larvae of *Pleurogrammus monopterygius*: A. 9.7 mm, B. 11.6 mm, C. 14.1 mm, D. 17.4 mm, E. 20.5 mm, F. 25.2 mm.

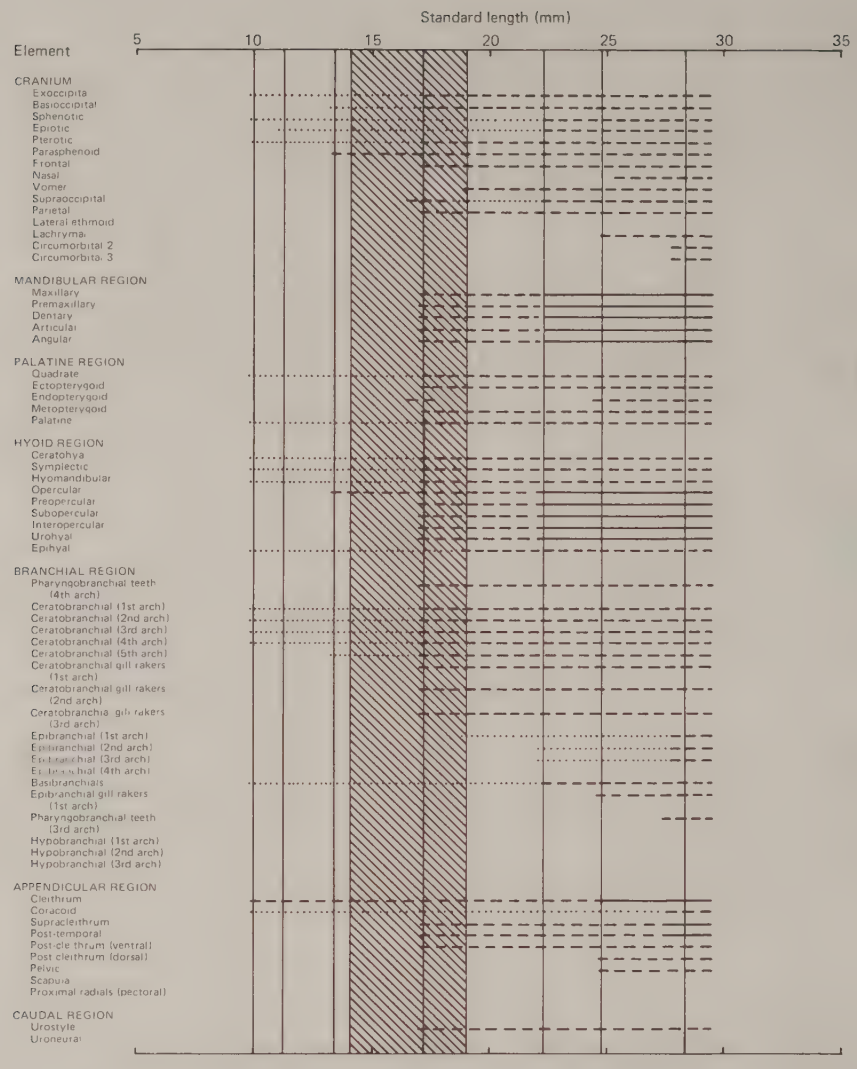

Figure 16.—Ossification of major bones in *Pleurogrammus monopterygius*. Symbols as in Figure 2.

from them mainly on the basis of pigment patterns. The larvae described here were collected in plankton and neuston nets in the Gulf of Alaska and the eastern Bering Sea. They were identified on the basis of earlier published descriptions and pigment patterns which could be traced back to small larvae from larger specimens which had distinguishing meristic characters.

Pigmentation—Yolk-sac larvae have a melanophore pattern which is seen in larger larvae with only slight changes. The forebrain, midbrain, and hindbrain are covered with large stellate melanophores, and a patch made up of several melanophores covers the upper preopercular region. In contrast to *Hexagrammos* larvae, the snout is unpigmented. A heavy line of melanophores connects to the midbrain pigment and runs along the dorsal midline from the nape to just anterior to the tip of the notochord. At the nape there are a few additional superficial melanophores just lateral to the dorsal midline pigment. Laterally there is a line of melanophores, mainly internal, just dorsal and ventral to the notochord. The dorsal line originates above and just anterior to the level of the anus, and the ventral line originates a few myomeres posterior to the anus. Both lines terminate anterior to the tip of the notochord. Ventrally, along the midline, a line of small distinct melanophores originates about 15 myomeres posterior to the anus and the melanophores increase in size and become more closely spaced until they terminate as a solid line just anterior to the notochord tip. In the area of the caudal peduncle, superficial lateral melanophores form a relatively heavily pigmented area. The dorsolateral surface of the gut cavity is heavily pigmented with stellate melanophores. As the larvae grow these melanophores cover more of the peritoneum, until by about 20 mm it is totally covered except along the ventral midline. Also as the larvae grow to about 14 mm a few small melanophores lie

around the posterioventral rim of the orbit and a few are added to the isthmus. The anterior part of the ventral midline pigment line becomes difficult to see as it is covered with flesh. By 20 mm the body is becoming densely covered with superficial melanophores that form a wide stripe over most of the lateral body surface by 25 mm. The dorsal midline pigment is more intense, as is the terminus of the lateral pigment at the base of the caudal fin. The finfolds, fins, and jaws are unpigmented throughout larval development.

Morphology—Morphometric measurements were taken on 84 larvae from 9.8 to 26.5 mm. During this length interval the body shape is typical of that of other hexagrammine larvae: They have blunt heads (head length increases from 18 to 25% SL), thin bodies (body depth increases from 13 to 19% SL), large eyes (eye diameter decreases from 56 to 39% HL), and short snouts (snout length increases from 9 to 16% HL). Preanal length increases from 33 to 50% SL. The notochord flexes between 14 and 19 mm. The major differences between body shape of *P. monopterygius* larvae and that of other hexagrammines are the slightly larger eye (by 5-10% head length) and the shorter snout (by about 2% head length), the shallower body depth at 15 to 25 mm and the larger size at which the increase in total length relative to standard length occurs (by 2-4 mm SL).

Developmental Osteology (Table 11)—A series of 43 larvae from 9.7 to 28.1 mm was cleared and stained to trace development of osteological features. Larvae of *P. monopterygius* are larger than other hexagrammine larvae at time of formation of most features. Relative to the sequence of development of meristic features seen in other hexagrammines, in *P. monopterygius* the median fins develop earlier and the vertebrae and pelvic fins develop later. Branchiostegal rays form at 11.1-15.1 mm and principal caudal rays form at 15.1-16.2 mm, although the uppermost principal ray still appears to be epaxial even in

Table 11.—Development of meristic structures of *Pleurogrammus monopterygius*. Specimens between dashed lines are undergoing notochord flexion. The first observation of count within adult range is underlined.

Standard length (mm)	Vertebrae[1]				Fins									Branchiostegal rays	Gill rakers	
	Precaudal		Caudal		Dorsal		Anal	Pectoral	Pelvic	Caudal						
										Upper		Lower				
	Partial	Complete	Partial	Complete	First	Second				Secondary	Principal	Principal	Secondary		Upper	Lower
11.1																
11.1						!								1		
11.2						!								1		
12.1						!								4		
12.2						!								4		
12.5						!								4		
13.1														4		
13.3														4		
13.6														5		
14.0														4		
14.1														5		
14.3														5		
15.1											4	6		5		
15.1											6	9		6		
15.1											4	6		6		
16.2				1				14			7	11		6		
16.2				1				15			7	11		6		3
16.3				1				14			7	11		6		
17.0				1				15		1	[2]7	11	1	6		
17.3				1				16		1	7	11	1	6		3
17.9	1			1				16		2	7	11	1	6		2
18.2	5			1				14		3	7	11	2	6		3
19.2	7			1				17		4	7	11	3	6		5
19.3	8			1				18		2	7	11	2	6		5
19.6	6			1		12	17	18		4	7	11	3	6		5
20.0	7	2		1		12	13	18		2	7	11	3	6		6
20.9	5	2		1		13	13	19		5	7	11	3	6		5
21.0	11	6		1	8	23	21	21		5	7	11	4	6		7
21.5	11	8		1	5	21	21	20		6	7	11	5	6		6
21.9	12	7		1	10	22	21	21		5	7	11	4	6		6
22.1	7	8		1	12	25	22	20		7	7	11	5	6		6
23.7	17	9	6	1	19	28	25	22	1,3	9	7	11	8	6		9
23.7	17	10	5	1	21	27	26	24	1,3	8	7	11	7	6		10
24.2	14	13	33	1	21	26	24	23	1,3	8	7	11	7	6		8
24.3	13	14	32	1	22	26	25	24	1,3	9	7	11	8	6		9
28.1	7	19	27	8	23	26	25	25	1,5	14	7	11	12	6	1	12

[1]Vertebrae in hexagrammids begin ossification as dorsal and ventral saddle-shaped pieces of bone which join each other laterally to form rings that further ossify to attain their definitive shape. Vertebrae were considered "partial" if ossification had begun, but the dorsal and ventral sections had not fused, after which a vertebra was considered "complete."

[2]Apparently the posteriormost upper secondary caudal fin ray, that is first present in this specimen, changes position to become the dorsalmost (eighth) principal caudal fin ray later in development.

the 28.3 mm specimen. The pectoral fin rays form next at 16.2-23.7 mm. The dorsal and anal fin rays form between 20 and 24 mm. The pelvic fins are the last fins to form at between 24 and 28 mm. The urostyle ossifies at 16.2 mm, the abdominal vertebrae start to form at 20 mm, and neither the abdominal nor caudal vertebrae are all fully ossified by 28.3 mm, the largest specimen of the series. First arch gill rakers start forming at 16.2 mm and continue to be added throughout the series examined.

On the smallest larvae stained, several bones of the skull (pterotic, exoccipital, sphenotic), suspensorium, and branchial area are present as cartilage. Most of the neural and hemal spines are cartilage, and there is an extended cartilagenous posterior coracoid process. During flexion most of the skeletal elements start to ossify and the hypurals form as cartilage. By the end of flexion, the neural and hemal spines have all ossified except for the last few. By 22 mm the bones of the jaws and those of the opercular region have attained their adult shapes. By 28 mm most of the bones of the head have started to ossify and there are a few teeth in the jaws. In other hexagrammines most bones have already attained their adult shapes by this size. The appendicular skeleton, except for the proximal pectoral radials, is mostly ossified. Dorsal and anal fin pterygiophores are present as cartilage. The epurals are present as cartilage; the rest of the caudal skeleton, including a pair of small uroneurals, is ossified. A foramen is present in both the dorsal and ventral hypural plates, indicating that each is composed of two elements (the upper of hypurals 3 and 4, the lower of the parhypural and hypurals 1 and 2). The uppermost dorsal principal caudal ray develops first as the posteriormost dorsal secondary caudal ray that moves caudally across the upturned tip of the notochord to become supported by the dorsal hypural plate.

DISCUSSION

Recent studies have demonstrated the efficacy of using larval fishes to elucidate relationships among several taxa and categories (Johnson 1974; Okiyama and Ueyanagi 1978; Kendall 1979). Among the Scorpaeniformes current studies are using larval characters of cottids to investigate relationships (Richardson 1981; Washington 1981; Richardson[2]). Although the systematics of the Scorpaeniformes need attention at every level, there appear to be three major suborders: The Hexagrammoidei which are derived from the Cottoidei, which in turn are derived from the Scorpaenoidei (Quast 1965). The interpretation of larval characters discussed below indicates that the hexagrammoid line arose from the cottoid line before the latter had differentiated much from the scorpaenoids. The most convincing synapomorphy of the Scorpaeniformes is the posterior extension of the third suborbital bone so that it connects with the preoperculum. Among the hexagrammids under consideration here, no differences in formation of this feature were noted: The third suborbital formed late in larval development and gradually extended posteriorly to reach the preoperculum during the juvenile stage.

A comparison of larval characters between presumed primitive scorpaenids and cottids and hexagrammids may help define the family Hexagrammidae, and determine its relationship to the other major groups of scorpaeniforms. Richardson (1981) listed presumed plesiomorphic characters of cottid larvae (which are assumed to be apomorphic with regard to the scorpaenoids) to include: Four strong preopercular spines, relatively deep compact body, presence of a preanal finfold, rounded snout, short pectoral fin, and a compact gut that lacks diverticula. Larval cottid group 4 (Richardson 1981), composed of *Hemilepidotus* spp. and *Scorpaenichthys marmoratus*, exhibited the plesiomorphic states of most of these characters. *Sebastes* seems to be representative of a generalized scorpaenoid. States of these characters as well as other features observable in the larvae that might help interpret relationships among these fishes are discussed below (Table 12).

Preopercular spines—Larvae of *Oxylebius pictus*, *Zaniolepis* sp., and *Ophiodon elongatus* possess preopercular spines, and other armature, but none is present in larvae of *Hexagrammos* spp. and *Pleurogrammus monopterygius*. In *Oxylebius pictus* four preopercular spines, similar to those seen in *S. marmoratus* and *Hemilepidotus* spp. (Richardson 1981), develop by the end of flexion. A fifth spine is added ventrally late in larval development (12-13 mm). In *Zaniolepis* sp. the preopercular spines are less pronounced, but up to seven develop by the late larval period. In *Ophiodon elongatus* larvae the preopercular margin is smooth until well after flexion when first two, then two more small, blunt spines develop. *Sebastes* larvae have 2-5 preopercular spines that are generally more robust than those on the other larvae considered here (Moser et al. 1977).

Body shape—*S. marmoratus* and *Hemilepidotus* spp. share the presumed plesiomorphic condition of a relatively deep body (Richardson 1981). In these larvae body depth increases with development from 15-19% SL in preflexion larvae to 32-35% in postflexion larvae (Richardson and Washington 1980). Larvae of *Oxylebius pictus* are deeper bodied during preflexion stages but about equal to these cottids after flexion. The other species described here have body depths from 13 to 18% SL during preflexion stages, but the depth only increases to a maximum of 25% in postflexion larvae of *H. lagocephalus*, whereas in the other species it stays < 22%. *Zaniolepis* sp. larvae seem equally slender bodied, although too few specimens were available for meaningful measurements. *Sebastes* larvae are quite deep bodied (> 20% SL at flexion) (Moser et al. 1977).

Preanal finfold—A small preanal finfold is present in early preflexion larvae of *O. pictus*. It remains visible in *Zaniolepis* sp. larvae until shortly after flexion. In *Ophiodon elongatus* larvae it is present throughout the larval period. In *Hexagrammos* sp. and *P. monopterygius* larvae it is present until the early postflexion stage. The preanal finfold is a presumed primitive character in cottid larvae, and is absent in *Sebastes* larvae (Table 12).

Snout shape—A basically rounded snout (8-28% head length) is present in larvae of all the taxa described here except *O. elongatus* (25-36% head length) which has a pointed snout starting in the early flexion stage. The snout is rounded in larvae of presumed primitive cottids, and is moderately pointed in *Sebastes* larvae (Table 12).

Pectoral fin development—Rays start to develop in the pectoral fin before flexion and shortly after the caudal fin rays develop but before development of rays in any of the other fins in all taxa described here. Pectoral fins reach their adult complements of rays during flexion in *Oxylebius pictus* and

[2]S. L. Richardson, Associate Ichthyologist, Gulf Coast Research Laboratory, East Beach Drive, Ocean Springs, MS 39564, pers. commun. November 1981.

Table 12.—Character states observed among hexagrammid larvae, in relation to their states in larvae of *Sebastes* spp. (Moser et al. 1977; Moser and Ahlstrom 1978) and in larvae of *Hemilepidotus* spp., a presumed primitive cottid (Richardson and Washington 1980; Richardson 1981).

Character	Character states			
	Sebastes spp.	*Hemilepidotus* spp.	Observed states in hexagrammids	Hexagrammid genera
Preopercular spines	3-5 strong spines	4 strong spines	3-7 spines	*Oxylebius*, *Zaniolepis*, *Ophiodon*
			no spines	*Hexagrammos*, *Pleurogrammus*
Body depth	>20% SL at flexion	>15% SL at flexion	<20% SL at flexion	*Ophiodon*, *Hexagrammos*, *Pleurogrammus*
			>20% SL at flexion	*Oxylebius*, *Zaniolepis*
Preanal finfold	absent	present	present (at least preflexion)	all
Snout shape	moderately pointed (>25% head length)	rounded (<25% head length)	rounded (<25% head length)	*Oxylebius*, *Zaniolepis*, *Hexagrammos*, *Pleurogrammus*
			pointed (>25% head length)	*Ophiodon*
Pectoral fin size	variable—reaching anus in some	short	short—not reaching anus	*Ophiodon*, *Hexagrammos*, *Pleurogrammus*
			long-reaching anus	*Oxylebius*, *Zaniolepis*
Gut shape	compact, not trailing	compact, not trailing	compact, not trailing	all
Head spines	on many bones	on few bones	none	all except *Zaniolepis*
			on few bones	*Zaniolepis*
Appendicular skeleton armature	spines on posttemporal (2) and supracleithrum (1)	reduced to bumps	spines on posttemporal and supracleithrum	*Oxylebius*, *Zaniolepis*
			none	*Ophiodon*, *Hexagrammos*, *Pleurogrammus*
Pelvic fin ray development sequence	before dorsal and anal fins	after dorsal and anal fins	concurrent with dorsal and anal fins	*Oxylebius*, *Zaniolepis*
			concurrent with first dorsal, after second dorsal and anal fins	*Ophiodon*, *Hexagrammos*, *Pleurogrammus*
Adult numbers of principal caudal fin rays	8+7	6+6	7+6	*Oxylebius*, *Zaniolepis*
			7+7	*Ophiodon*
			7+8–10	*Hexagrammos*
			8+11	*Pleurogrammus*
Adult caudal fin skeleton[1]	hypurals 1 and 2 fused, hypurals 3 and 4 fused, hypural 5 present	parhypural and hypurals 1 and 2 fused, hypurals 3 and 4 fused, hypural 5 absent	parhypural free from fused hypurals 1 and 2	*Ophiodon*
			parhypural and hypurals 1 and 2 fused	*Oxylebius*, *Zaniolepis*, *Hexagrammos*, *Pleurogrammus*
			hypural 5 present	*Oxylebius*
			hypurals 3 and 4 fused	all
Anal fin spines	3 strong	no spines	3-4 strong	*Oxylebius*, *Zaniolepis*
			0-3 weak	*Ophiodon*, *Hexagrammos*, *Pleurogrammus*
Pigment pattern	light	heavy	heavy	all

[1]*Hemilepidotus*, pers. obs.

Zaniolepis sp. but continue to add fin rays until late in the larval period in the other taxa. The pectoral fin is large in *O. pictus* and *Zaniolepis* sp. larvae, reaching posteriorly well beyond the anus in late larvae. In the other taxa, however, the pectoral fin is small, never reaching the level of the anus. In presumed primitive cottids the larval pectoral fin is short, and it is variable in length among species of *Sebastes* (Table 12).

Gut shape—The gut in hexagrammid larvae is compact without diverticula or a trailing hindgut. The preanal length varies from 42 to 60% SL, with *Ophiodon elongatus* having the longest preanal length (52-60% SL). The hindgut of *Zaniolepis* sp. seems slightly enlarged and bulges slightly before flexion is complete. The larval gut is compact in both presumed primitive cottids and in *Sebastes* (Table 12).

Appendicular skeletal armature—*Sebastes* larvae generally possess numerous spines on the head and on the bones of the appendicular skeleton (Richardson and Laroche 1979). Some cottid larvae likewise possess such armature, but it is generally not as sharp or extensive. In hexagrammid larvae the shoulder region is unarmed, except in *Oxylebius pictus* and *Zaniolepis* sp. where small spines develop on the posttemporal and on the supracleithrum.

Pelvic fin development—In larvae of *O. pictus* and *Zaniolepis* sp. the pelvic fin bud is first seen during flexion; in *Ophiodon elongatus* it is first seen in early postflexion larvae and in *Hexagrammos* spp. and *P. monopterygius* not until well after flexion. In the latter three genera the pelvic fin does not reach its adult complement of rays until all other fin rays, except the secondary caudal rays, are present. In *Oxylebius pictus* and *Zaniolepis* sp. pelvis fin ray counts are complete shortly after flexion. In *Sebastes* the pelvis fin develops before the dorsal and anal fins (Moser et al. 1977). Hexagramminds retain the presumed plesiomorphic scorpaeniform pelvic fin ray count of I,5, whearas in cottids the count is reduced in many genera with I,3, being the most common number (Richardson and Washington 1980.).

Principal caudal fin rays—Ahlstrom and Moser (1976) emphasized the stability of principal caudal fin ray counts within higher categories of fishes. *Sebastes* has 8+7 principal caudal fin rays (Moser et al. 1977); the number is reduced to 6+6 in cottids, with several taxa having even fewer. *Oxylebius pictus* and *Zaniolepis* sp. have 7+6 principal caudal fin rays, *Ophiodon elongatus* has 7+7, the count varies among the species of *Hexagrammos* from 7+8 to 7+10, and *P. monopterygius* has 8+11. The progression of increase in principal caudal rays seems to parallel an increase in free-swimming habit as opposed to rest-and-dart behavior seen among other taxa. This may also be related to a decrease in the use of the pectoral fins in propulsion, which appears to be of primary importance in many cottids and *Oxylebius pictus*.

Caudal fin skeleton—In the hexagrammid taxa there is a variable number of principal caudal fin rays, and a variable number of elements in the caudal fin skeleton resulting from both loss and fusion of elements. One uroneural was present, as in *Sebastes* (Moser and Ahlstrom 1978), a reduced condition compared with the basic perciform number of 2 (Gosline 1961) (Table 13). Apparently this represents a loss of one uroneural since no evidence of fusion similar to that in *Coryphaena* (Potthoff 1980) was seen. Three epurals developed in all taxa examined here. The parhypural fused to the lower hypurals in all larvae except *Ophiodon elongatus*. In those taxa where it fused, a foramen was seen as the ventral hypural plate ossified. Hypurals 1 and 2 fused in all taxa examined, as occurs in *Sebastes* (Moser and Ahlstrom 1978). Thus in *Oxylebius pictus*, *Zaniolepis* sp., *Hexagrammos* spp., and *P. monopterygius* there is a ventral hypural plate composed of the parhypural and hypurals 1 and 2. Hypural 5 was seen only in *O. pictus*; it is characteristic of the basic perciform pattern (Gosline 1961) and is present in *Sebastes* (Moser and Ahlstrom 1978). Hypurals 3 and 4 are fused to form a dorsal hypural plate in all taxa examined here as they are in *Sebastes* (Moser and Ahlstrom 1978). During development, hypural fusion was usually indicated by separate centers of ossification or gaps which later filled in with bone. Two autogenous hemal spines are present in all taxa examined, as they are in *Sebastes* (Moser and Ahlstrom 1978) and in basic perciforms (Gosline 1961). The urostyle was the first bone to ossify in the caudal region and there was no indication of it being composed of more than one element. On its anteriodorsal surface a pair of small spines developed as in *Coryphaena* (Potthoff 1980, fig. 21). A modified neural arch without a neural spine developed on the centrum anterior to the urostyle. This appeared to be composed of two serial sections; the anterior one developed in cartilage between the last and next-to-last full centrum. These two sections remained separate throughout the largest material examined of *O. pictus* and *Ophiodon elongatus*. In *P. monopterygius* and *Hexagrammos* spp. there was generally only one section, but two, or indications of a fusion of two, were seen in some specimens.

Anal fin spines—*Sebastes* has three strong anal spines (Moser et al. 1977), while cottids have only soft rays in the anal fin (Richardson and Washington 1980). *Oxylebius pictus* and *Zaniolepis* sp. have 3 to 4 strong anal spines, but the rest of the taxa described here have a variable number (0-3) of spines that are so weak that it is difficult to distinguish between spines and soft rays. The dorsal fin spines in these taxa are also weak, particularly in *Hexagrammos* spp. and *P. monopterygius*.

Pigment patterns—Larvae of *Sebastes* are generally lightly pigmented until well after flexion, except in some species with heavily pigmented pectoral fins (Moser et al. 1977). Cottid larvae are variable in pigment, but the presumed primitive cottid, *Scorpaenichthys marmoratus*, has a heavily pigmented larva (Richardson 1981). All hexagrammid larvae develop heavy pigmentation over much of the body. This is presumably related to their epipelagic prejuvenile stage, when similar pigment is seen in other fish that have such a stage. In life these fish have iridescent dark green to blue upper bodies and silvery lower bodies, but this pattern disappears on preservation. Since this pigment pattern is highly adaptive for fish in this habitat, it may be of limited value in interpreting relationships, as it is subject to convergence. *Hexagrammos* spp. and *P. monopterygius* are the most heavily pigmented hexagrammids, and among the species of *Hexagrammos* a progression from less to more pigment is: *H. stelleri*, *H. decagrammus*, *H. lagocephalus*, and *H. octogrammus*. The highly pigmented pectoral fins of *O. pictus* and *Zaniolepis* sp., are unusual but not unique among scorpaeniforms. Similarly pigmented pectoral fins are seen in some *Sebastes* (Moser et al. 1977), *Anoplopoma fimbria* (Ahlstrom and Stevens 1976), and the psychrolutid cottids (Richardson 1981).

In summary, no single larval character was found which clearly indicated that the hexagrammids are a monophyletic group. Also, although hexagrammid larvae can be distinguished from *Sebastes* and cottid larvae on the basis of several characters, little additional evidence on the relationships among these groups was provided. For example, the pattern of fusion and loss of bones in the caudal skeleton showed that all conditions seen in the hexagrammids and *Hemilepidotus* could

Table 13.—Major components of the caudal fin skeleton in hexagrammids, *Hemilepidotus*, and *Sebastes* compared with the basic perciform pattern. "+" represents presence of an element, "o" its absence. Braces indicate fusion of elements. Three epurals and an autogenous hemal spine on each of the two vertebrae immediately anterior to the urostyle are present in all listed taxa.

Component	Basic perciform pattern[1]	*Sebastes*[2]	*Ophiodon*	*Oxylebius*	*Zaniolepis*	*Hemilepidotus*[3]	*Hexagrammos*	*Pleurogrammus*
Uroneural 1	+	+	+	+	+	+	+	+
Uroneural 2	+	o	o	o	o	o	o	o
Parhypural	+	+	+					
Hypural 1	+			+	+	+	+	+
		+	+					
Hypural 2	+							
Hypural 3	+							
		+	+	+	+	+	+	+
Hypural 4	+							
Hypural 5	+	+	o	+	o	o	o	o
Principal caudal fin rays								
dorsal	9	8	7	7	7	6	7	8
ventral	8	7	7	6	6	6	8-10	11

[1]Gosline (1961).
[2]Moser and Ahlstrom (1978).
[3]Pers. obs.

be derived from that of *Sebastes*, which in turn could be derived from the basic perciform pattern. However, the pattern in *Hemilepidotus* was identical to that in *Hexagrammos* and *Pleurogrammus*, while it appeared that the patterns in *Ophiodon* and *Oxylebius* were each derived from the *Sebastes* pattern independently. The need for analysis of more characters among more members of the cottids and scorpaenids is indicated.

Among the hexagrammids, three groups of taxa were demonstrated by larval morphology. Analysis of the phyletic relationships among these groups of taxa must await a thorough examination of the adults. Nevertheless, based on larval appearance, *Oxylebius* and *Zaniolepis* are quite similar as are *Hexagrammos* and *Pleurogrammus*, while *Ophiodon* shares few characters in common with either of these groups.

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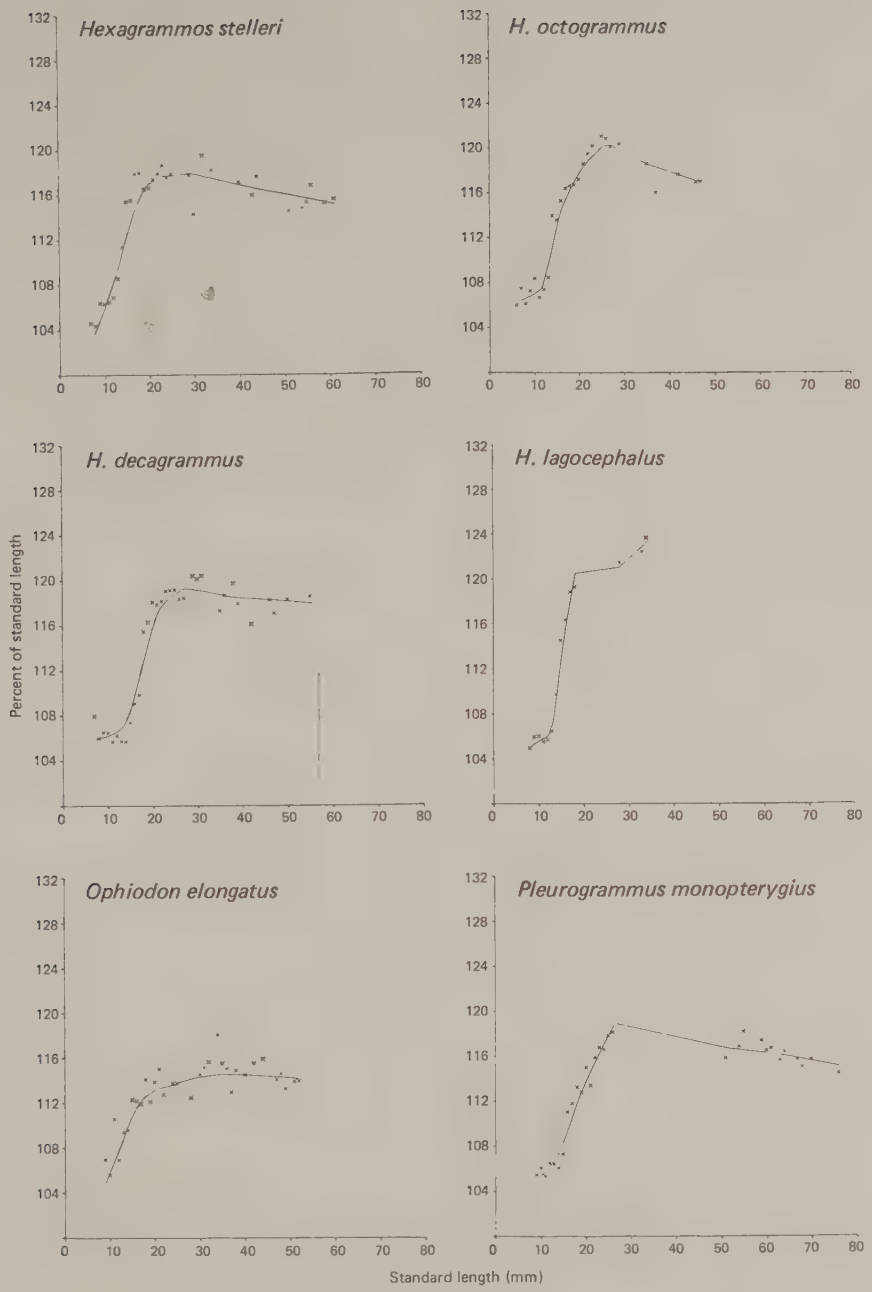
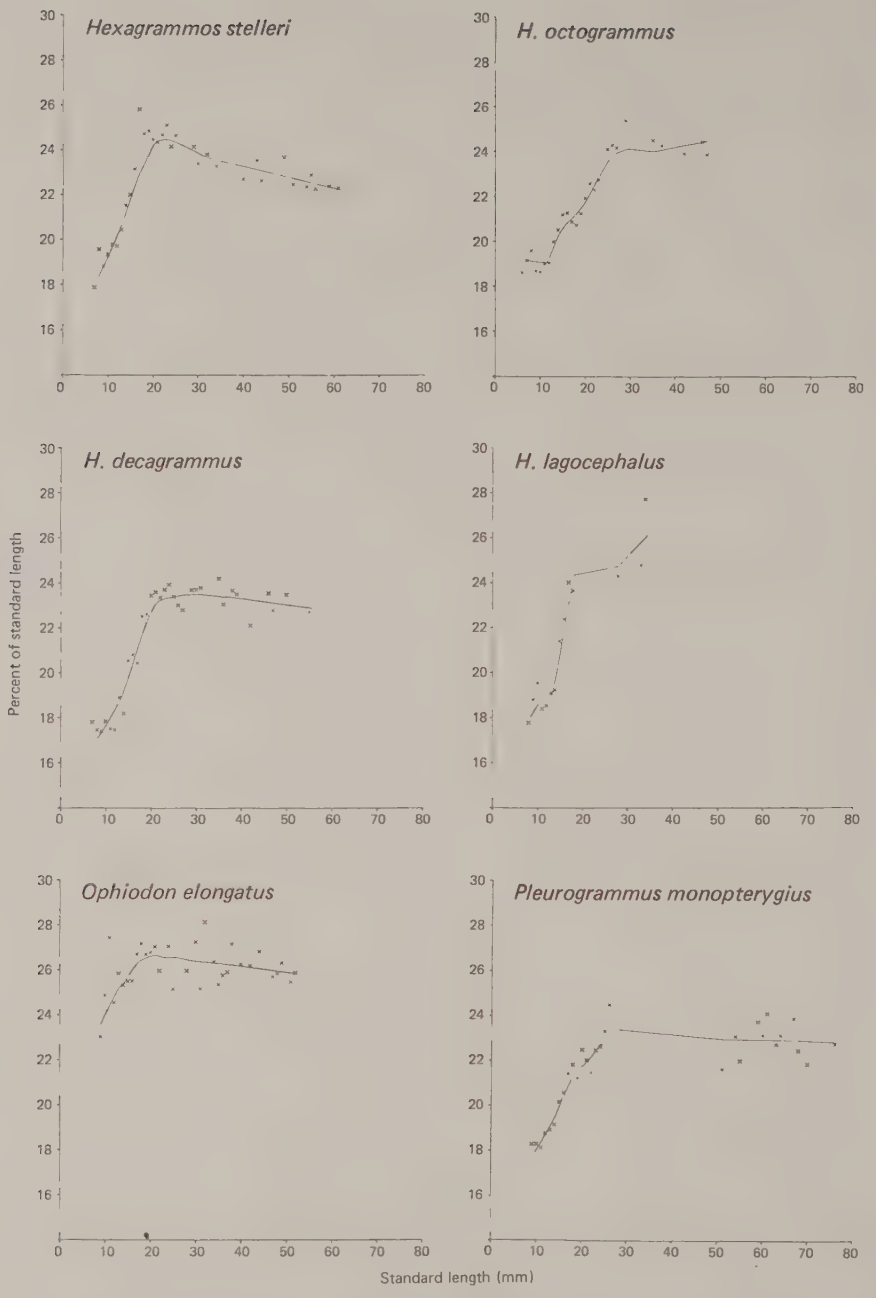
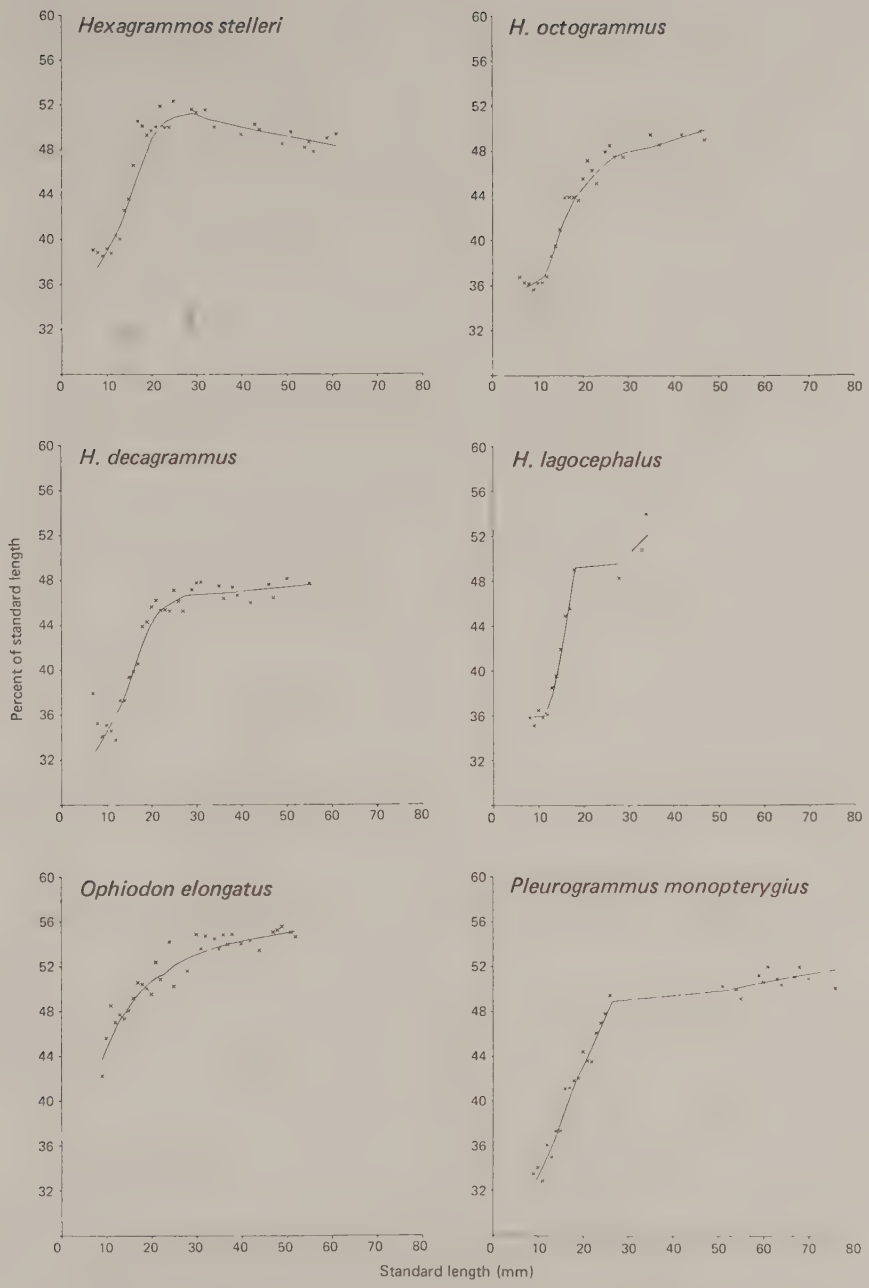


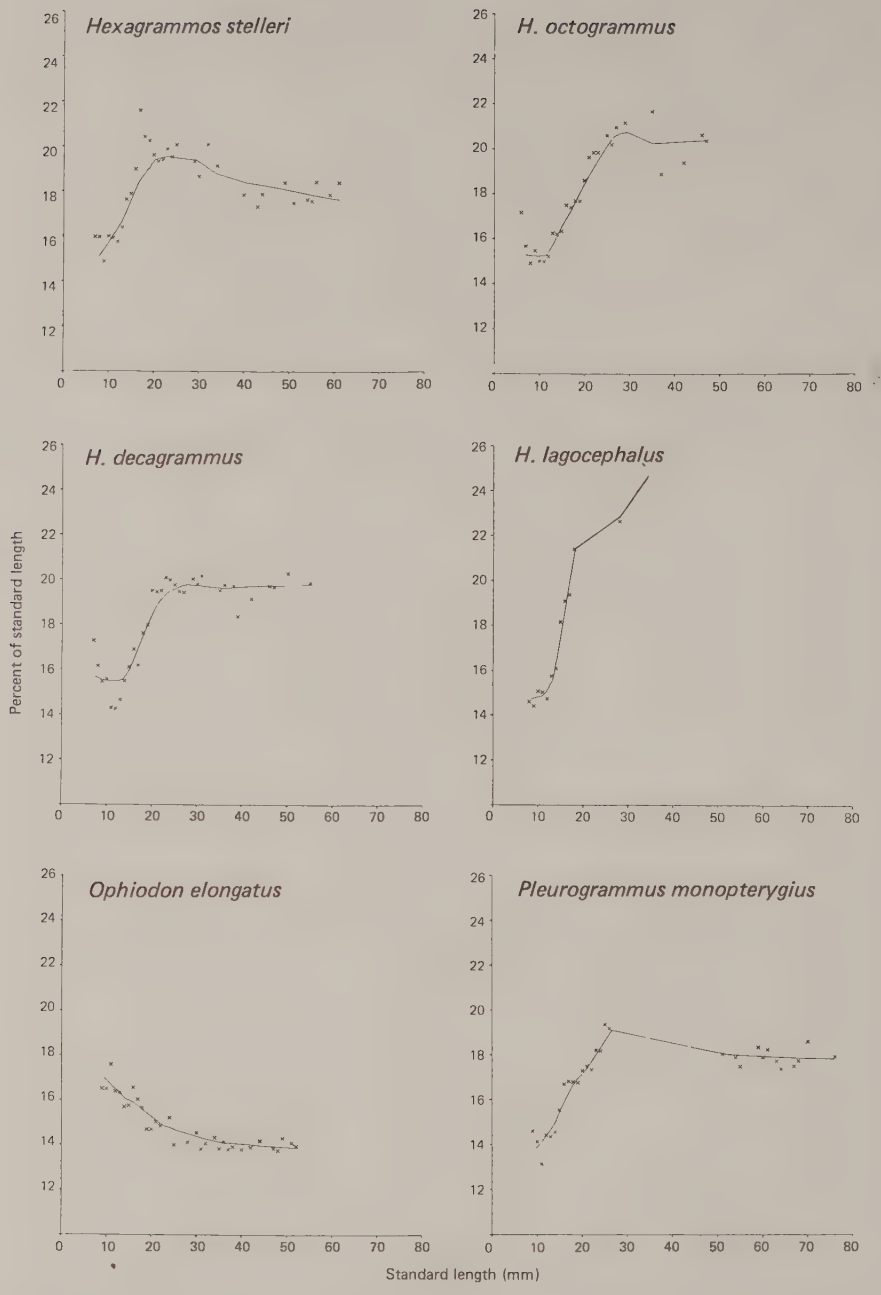
Appendix Figure 1.—Total length as a percentage of SL versus SL during development of six species of hexagrammids.



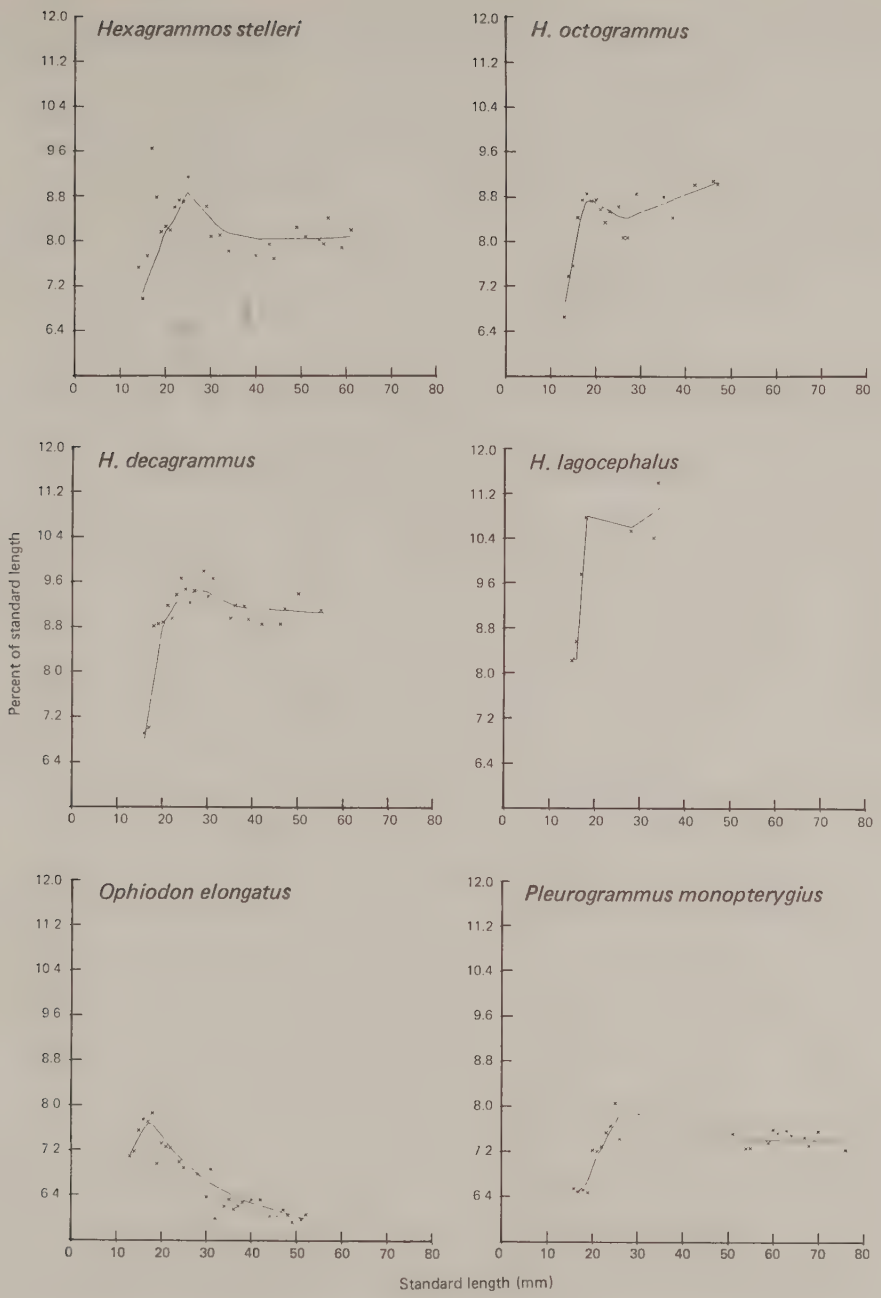
Appendix Figure 2.—Head length as a percentage of SL versus SL during development of six species of hexagrammids.



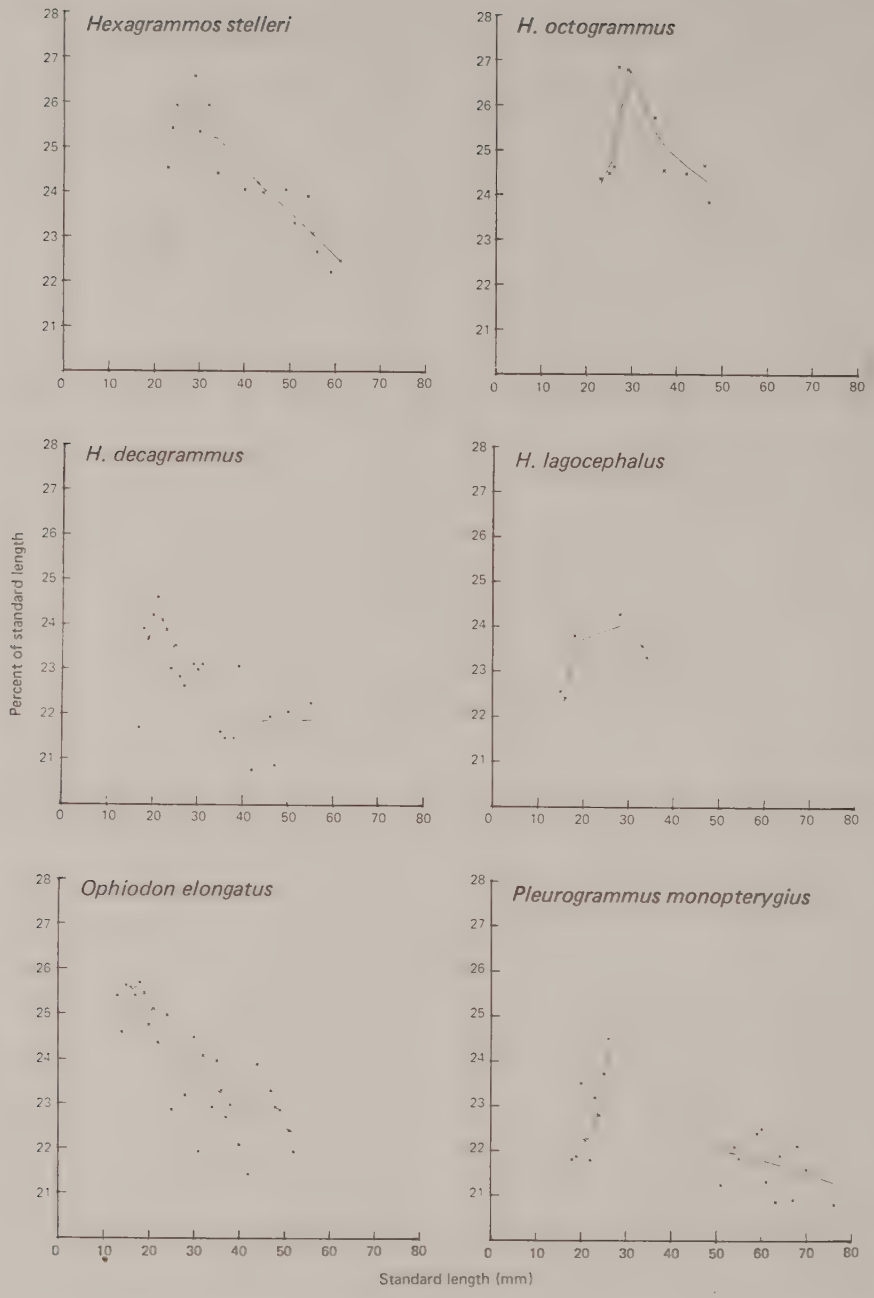
Appendix Figure 3.—Preanal length as a percentage of SL versus SL during development of six species of hexagrammids.



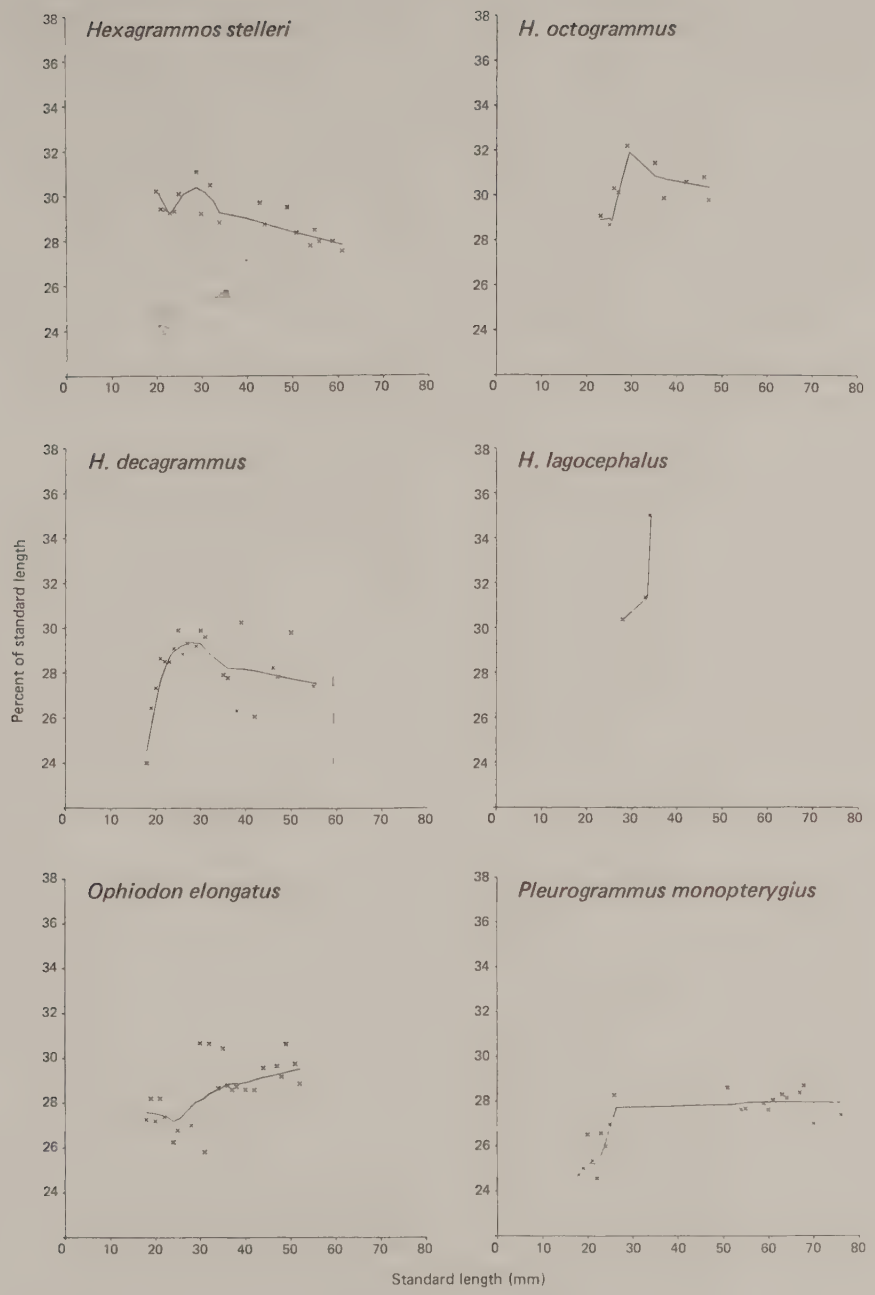
Appendix Figure 4.—Body depth at pectoral fin base as a percentage of SL versus SL during development of six species of hexagrammids.



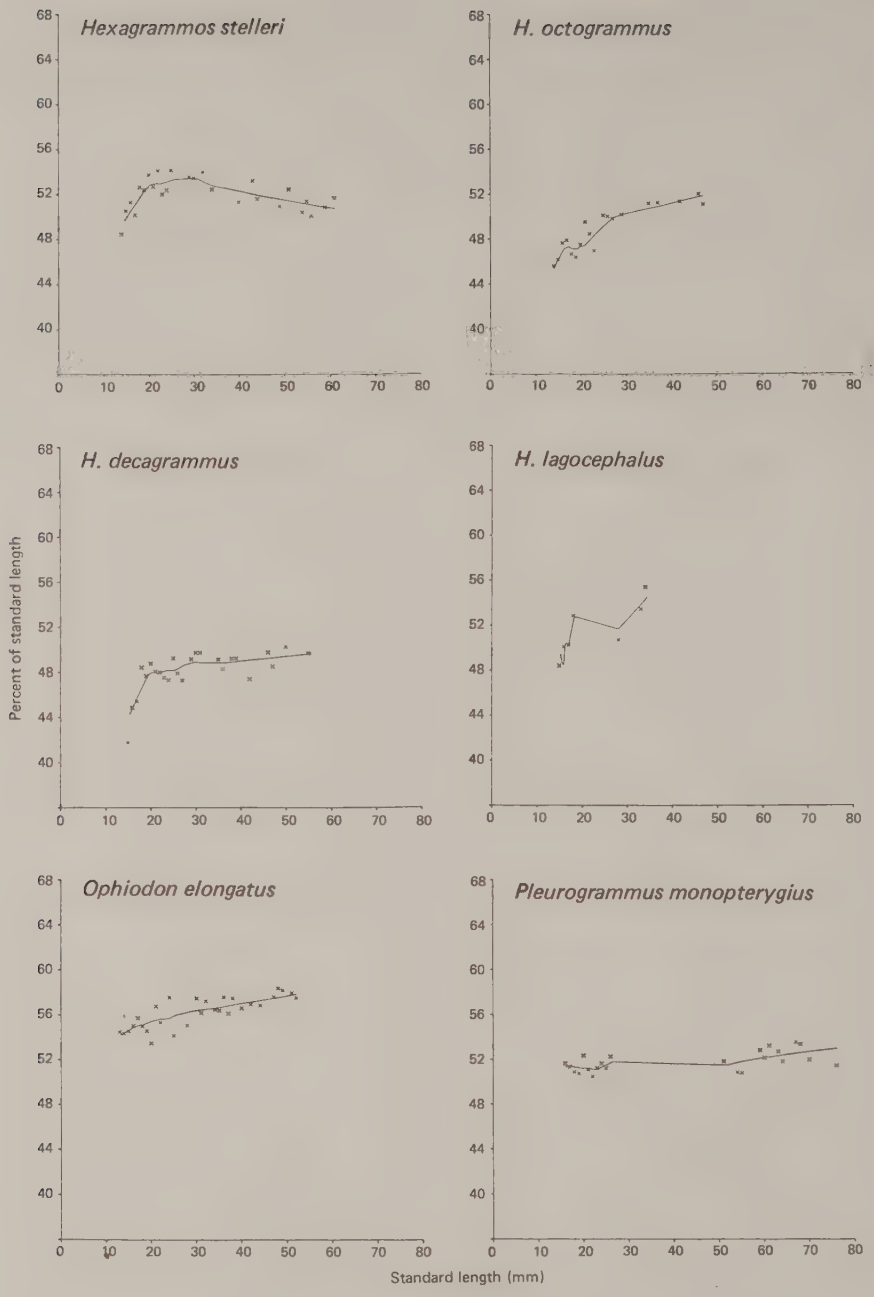
Appendix Figure 5.—Body depth at the caudal peduncle as a percentage of SL versus SL during development of six species of hexagrammids.



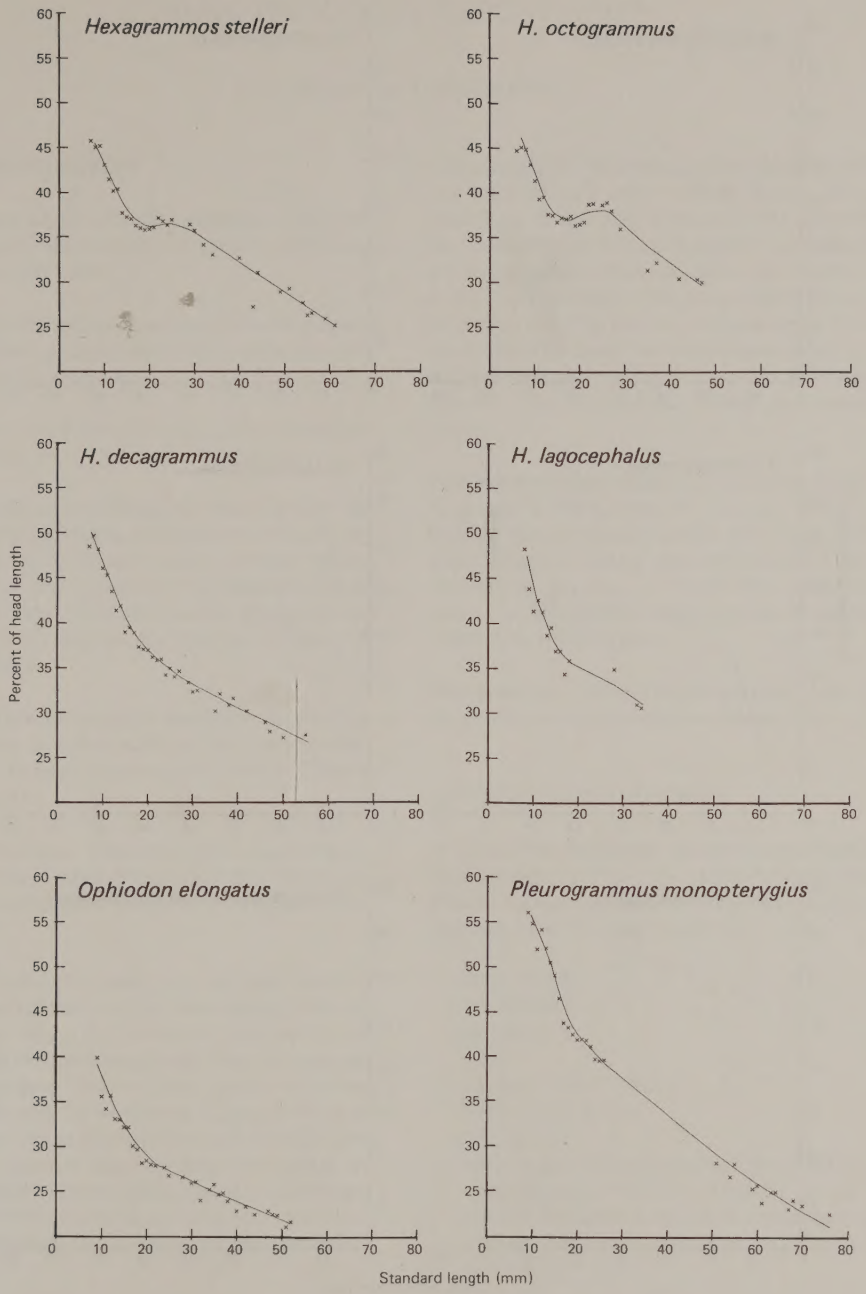
Appendix Figure 6.—Snout to dorsal fin origin length as a percentage of SL versus SL during development of six species of hexagrammids.



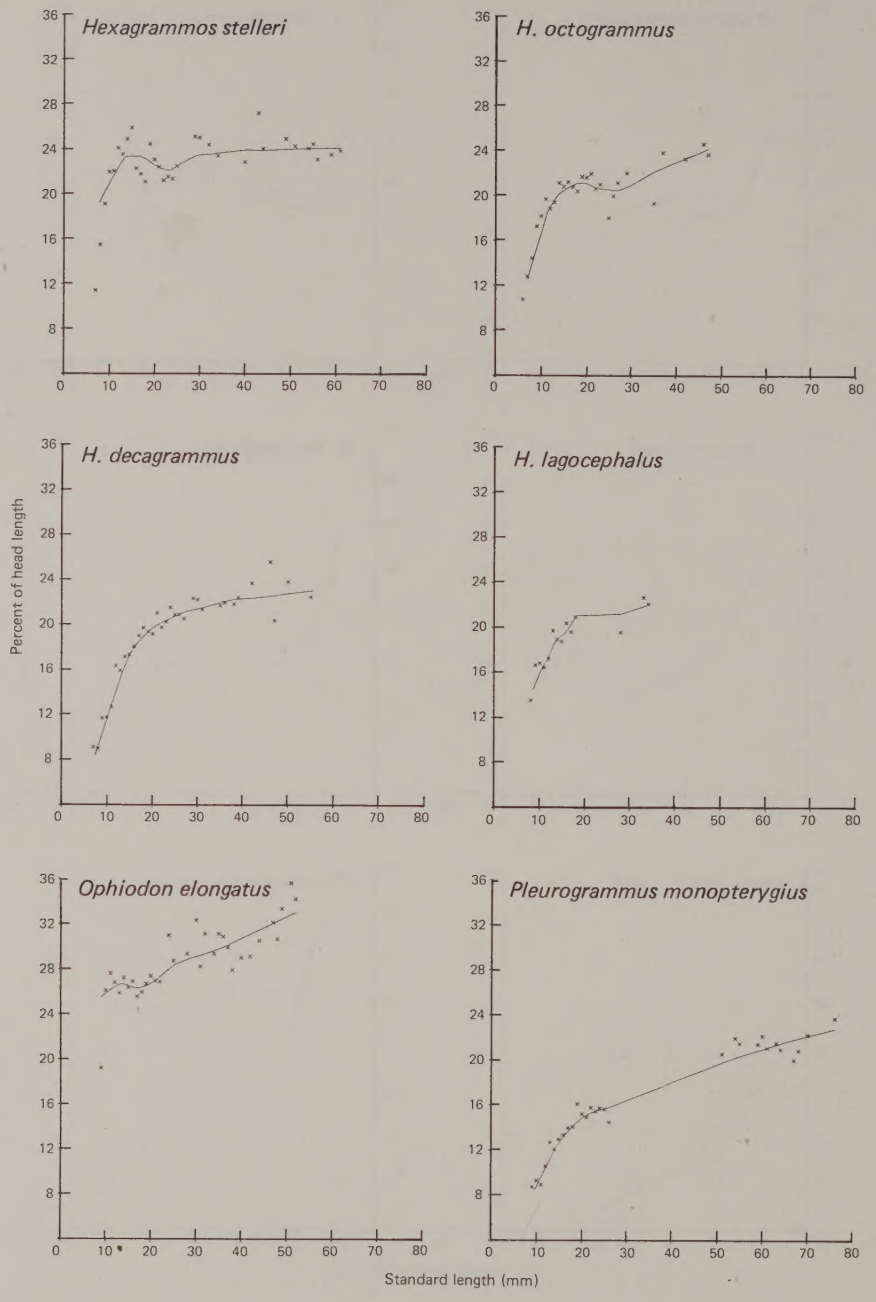
Appendix Figure 7.—Snout to pelvic fin origin length as a percentage of SL versus SL during development of six species of hexagrammids.



Appendix Figure 8.—Snout to anal fin origin length as a percentage of SL versus SL during development of six species of hexagrammids.



Appendix Figure 9.—Eye diameter as a percentage of head length versus SL during development of six species of hexagrammids.



Appendix Figure 10.—Snout length as a percentage of head length versus SL during development of six species of hexagrammids.

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